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FACTORS AFFECTING THE LOCAL DISTRIBUTION OF BLUE GROUSE ON A BREEDING RANGE

by

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ABSTRACT

The dispersion of a population of blue grouse was analyzed using data from a breeding range on east-central Vancouver Island. During the summers of 1959-1962, the locations, densities, vegetative preferences, and behaviour of grouse were studied using several habitats with varying densities of vegetation. A removal experiment was performed in different habitats to test the effect of interaction and selection of habitat on the dispersion of males.

All adult males and a few yearling males were territorial, and territories were spaced in a near-uniform pattern. Within a given season, males removed from their territories were seldom replaced by other adults, suggesting that no surplus of non-territorial adults was present. About half of the yearling males were prevented from establishing territory by the presence of adults, and these yearlings were attracted to the vicinity of territorial males. The location of territories by newly-adult males did not depend significantly on the number of territories already present, even though the tendency toward uniform spacing was preserved. Comparison with other studies indicated that territory size and possibly the fraction of yearling males in the population were inversely related to the density of males. Females restricted their movements while on the breeding range but were not territorial. No pair-bonds were observed but females stayed near territorial males prior to nesting. After the hatch, the locations of females and broods bore no relation to each other or to the positions of males. Interaction apparently had no effect on breeding numbers.

All birds preferred sparse vegetation to dense. When compared to randomly-chosen points, territories were found more often in areas with

sparse vegetation, elevated points, and patches of open ground. Within open habitats, nests were usually located where cover by logs, stumps, and ground-level vegetation was high, and cover by dead plants and litter was low. Broods were associated with moist areas and other areas having heavy cover by vegetation at the ground level.

Chicks apparently dispersed widely between their first and second summers. In their third summer, males usually returned within one-half mile of the positions they used as yearlings. Once territories were established, the owners returned to them in succeeding summers. Females one year and older showed a fairly accurate return to their previous locations.

The dispersion was described somewhat theoretically by considering the summer population to be grouped into two types of aggregations. The first, found in the earlier half of the summer, was caused by the attraction of yearling males and lone females to territorial males. Later, hens with their broods were the dominant groupings. The spacing, movements, and habitat preferences seemed to be adaptations allowing such populations to rapidly exploit new habitats.

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INTRODUCTION

This thesis attempts to describe and explain dispersion, or local distribution in a population of blue grouse, Dendragapus obscurus fuliginosus, on its summer range. The effects of social interaction and habitat selection on dispersion of territorial males, non-territorial males, females, and juveniles are examined. Particular attention is paid to certain questions as yet little studied on this species. Some of these questions are:

1. How fully can the dispersion of the grouse be explained by intraspecific interaction?
2. How important is this interaction in the control of numbers?
3. Other than interaction, what factors affect the dispersion of the population?
4. How important to spacing are summer movements and the dispersal of juvenile birds?
5. What sort of social organization is shown by these birds on their breeding range?

These questions were framed with the male blue grouse in mind and the report stresses explanation of dispersion in the males. Dispersion of females and young is discussed more briefly.

Since information on dispersion in birds is scattered through the literature, a complete review of the subject will not be included here. Many studies on territoriality, habitat selection, and social organization have appeared and relevant papers will be mentioned throughout the text. The term "dispersion" is used in this report as in Wynne-Edward's (1962) book which is the most recent general work on dispersion. The most recent and detailed work on the biology and ecology of the coastal blue grouse is that of Bendell (1954). The reader should keep in mind that these coastal birds show an altitudinal migration, descending from upland winter range at about the end of March and ascending from July through September.

DESCRIPTION OF STUDY AREA AND VEGETATION

The study area was located in the Quinsam Lakes region of Vancouver Island approximately eleven miles southwest of Campbell River, British Columbia. Fig. 1 shows the region covered, a roughly circular area approximately three miles in diameter, bounded on the south by Middle Quinsam Lake. The study area used by Bendell from 1950 to 1953 lies six miles to the east (Bendell, 1954).

Most of the area consists of low hills separated by temporary ponds, small streams, swamps, or peat bogs in the depressions. Prior to logging and burning the area possessed a humid littoral climate with an average annual temperature of about 50° Fahr. and rainfall of 40-80 in. per year. The original soil was concretionary brown or minimal podzol (Krajina, 1959; 1964). Throughout the study there was a greater range in temperature and humidity on the study area than in surrounding forested sections. At this time it was also clear that fire and erosion had much reduced the upper layers in the soil profile.

Originally the area was mature forest, defined by Rowe (1959) as the southern coast section of the Coastal Forest Region. By Krajina's classification the area was a mixture of Douglas fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) bioclimatic zones. Two severe forest fires have affected the area (Fig. 1) and the vegetation is now that of early successional stages. The extent of the fires, the type of regeneration, and the presence of plantations of Douglas fir (resulting from reforestation programs) have caused the area to develop four main types of vegetation. On the basis of structure and density these are called Very Open, Open, Dense, and Very Dense.

The Very Open and Open types were found within the area burned in

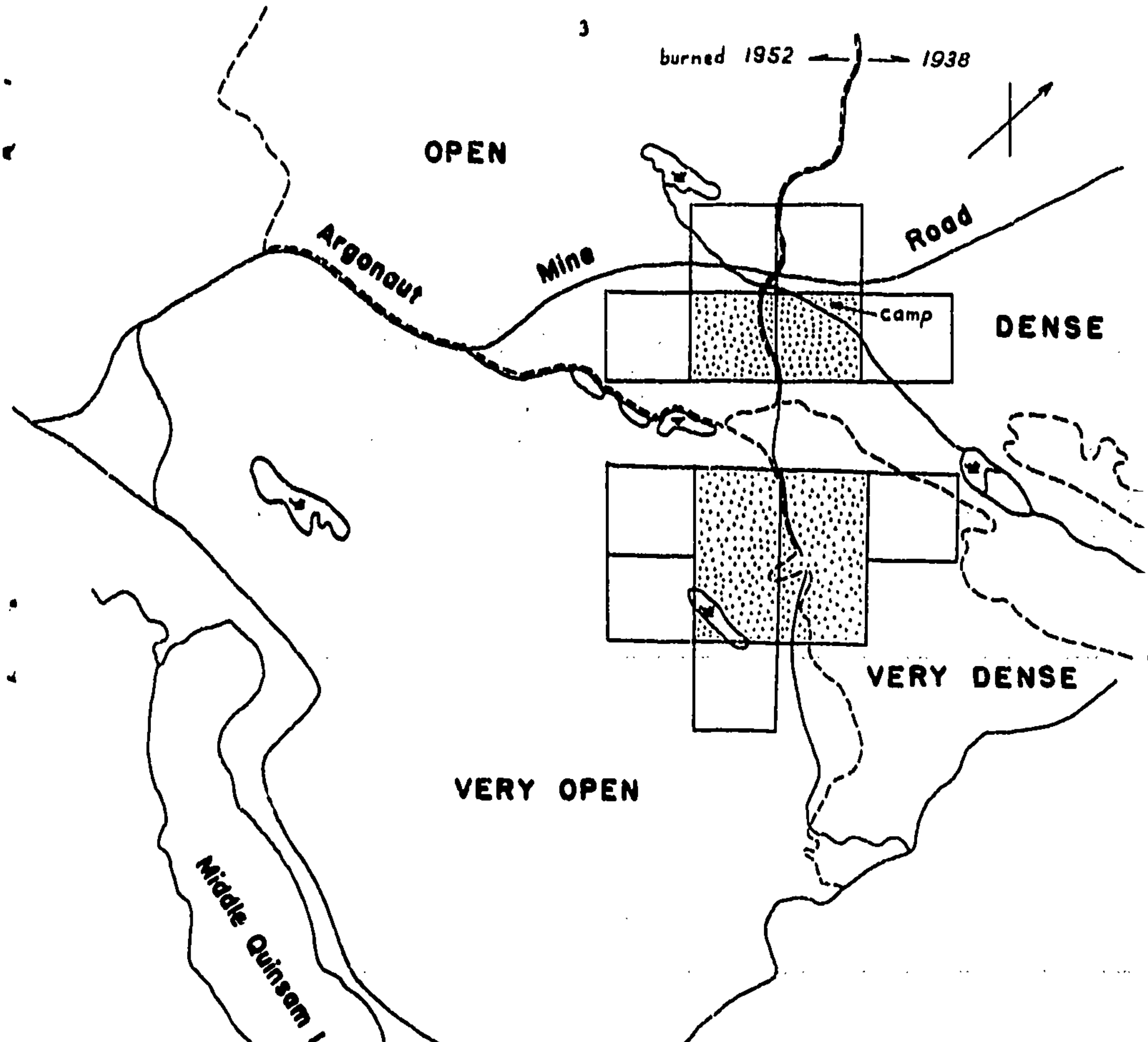


Figure 1. Study area, showing plots (see text), main zones of vegetation, lakes and swamps. Dashed lines separate vegetational zones. Scale: 1/8" = 200'.

1952. Very Open parts were those showing a light cover of willow (Salix spp., mainly S. sitkensis) and practically no coniferous cover, even on some sections where fir planting had been attempted in 1958 (Fig. 2). This was the most common type over the study area. Open areas showed a slightly heavier deciduous cover and much more conifer. These areas were reforested in 1953 (Fig. 3) and, as in the first type, most of the coniferous cover was Douglas fir.

The Dense and Very Dense types were located within the boundaries of the 1938 fire and apparently obtained their coniferous cover through natural as well as artificial regeneration. The cover by deciduous trees was about the same in these two types and was heavier than that of the open types. The two differed in amount of conifer. The Dense areas were partly replanted and showed a mixture of red cedar (Thuja plicata), fir, and hemlock (Fig. 4). The Very Dense areas showed the heaviest cover by conifers and, although several species were present, the mixture was dominated by hemlock (Fig. 5). Some planting had been done here but most regeneration seemed to have been natural. This was the least common type over the study area.

Hundred-foot line-intercepts and yard-square quadrats were used to describe the four types of vegetation more rigorously. The length of each portion of a tree or other major structure that was "cut" by a line was measured to the nearest 0.1 ft., and the height to the nearest 0.5 ft. The quadrats were located at 20 ft. intervals along the lines and, on these, the area covered by logs, rocks, litter, bare soil, and each plant species was estimated to the nearest 10%. Species covering less than 10% of a quadrat were listed only as being present, and were later given an arbitrary value of 2 or 5% depending on the size of the species. Some plant species

Figure 2. Photograph of Very Open habitat, fall, 1962. Rod shown is divided into one-foot intervals.

Figure 3. Photograph of Open habitat. Some Dense habitat shown in background.

Figure 4. Photograph of Dense habitat.

Figure 5. Photograph of Very Dense habitat.

and other elements were estimated by both methods and, in these cases, the quadrat figures were remarkably close to the more accurate line-intercept figures. The more important totals are given in Table I below and further information from these analyses is given in the appendices.

Table I. Description of vegetative and other cover on four main habitats from line-intercepts and quadrats measured in September, 1962. Figures in first four rows are from lines, last three rows from quadrats.

Structural element	Type of vegetation			
	Very Open	Open	Dense	Very Dense
Coniferous species	2%	28%	45%	75%
Deciduous species	13	16	26	24
Salal (<u>Gaultheria shallon</u>)	10	15	22	31
Logs and stumps	14	11	24	15
Number of lines	13	13	13	11
Number of quadrats	71	63	68	60
Ground vegetation	21%	20%	36%	44%
Bare ground and rock	24	17	3	5
Duff and litter	68	73	81	83

Willows are the main deciduous species referred to in the table but some alder (<u>Alnus rubra</u>) and huckleberry (<u>Vaccinium</u> spp.) are included in this category. Salal is included since it was the dominant species at the ground level (64% of ground vegetation, on the average). Bracken fern (<u>Pteridium aquilinum</u>) can be seen in the photographs which were taken in the fall. Since this species is a late-developing one, and since I was been omitted from the table. The duff and litter category includes dead leaves and other parts of plants, mosses, rotten wood, and similar material. The change in total cover by trees and shrubs from Very Open to Very Dense, neglecting any overlap of deciduous and coniferous species, gives some idea of the density of the brush. The totals ar , starting with the Very Open, 15%, 44%, 71%, and 99%.

It is difficult to show the gradation in these habitats even with the help of photographs. Because the four types are mentic.ed often in the text and because the density of vegetation was a basic factor determining the spacing of grouse, I include a diagrammatic representation of the four habitats which should show the differences more clearly (Fig. 6). For each habitat the line-intercept closest to the average was used in the figure (some measurements were adjusted slightly to make the coverage along the line more like the average). Some species were omitted and the remainder were categorized just as in Table I.

Other types of vegetation were obvious on the area but occurred less frequently. Some of these were:

1. Dense stands of pure alder or willow, usually in wet depressions.
2. Riparian thickets of various shrubs such as *Cornus occidentalis*, *Rubus spectabilis*, and *R. parviflorus*.
3. Dense sedge areas (*Carex* spp.) in moist depressions.
4. Swamps in areas of slowly moving water (*Lysichitum americanum*, *Oponlanax horridus*, etc.)
5. Bogs in areas of stagnant water (Sphagnum spp., *Ledum groenlandicum*, *Pinus contorta*, etc.)

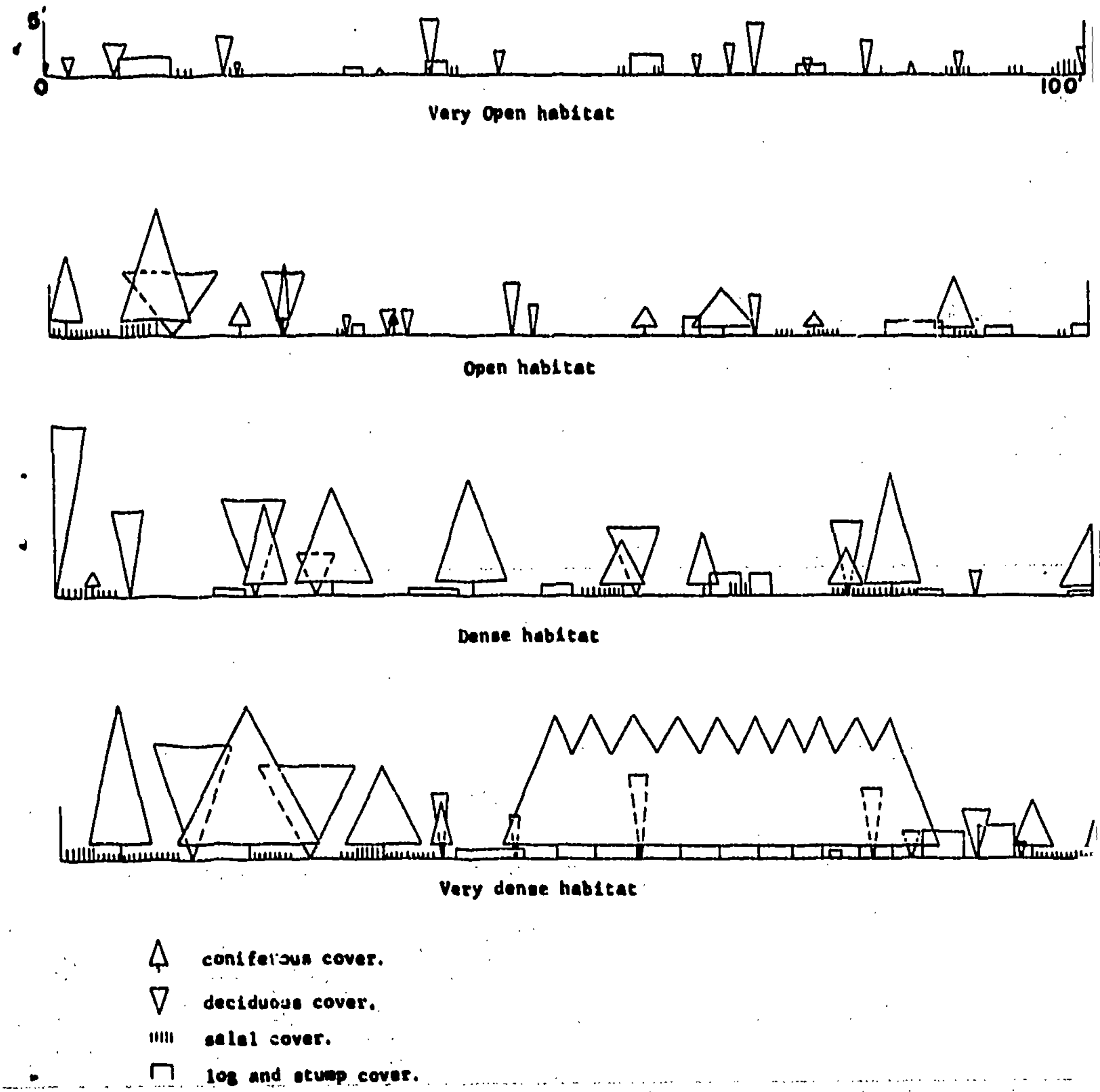


Figure 6. Diagram showing an average line-transect for each major type of habitat over the study area, spring aspect, 1962.

METHODS

Bendell's (1954) procedures were used for observing, handling, and individually banding the grouse. So that their locations could be mapped, all observations were related to known points on the study area. Captured or collected birds were classified as juvenile, yearling, or adult by their outer rectrices and last two primaries (Bendell, 1955). Weights and bursal depths were used in some cases. Each time a grouse was discovered in the field, notes were made on its behaviour, its position relative to any neighbours, and the habitat immediately around it.

An experiment was used to test the effect of interaction and habitat selection on the dispersion of males. During the summers of 1959 through 1962 males were removed from two 46-acre plots, each 1000 by 2000 ft., starting as early in the breeding season as possible. This was done mainly to establish whether removed males would be replaced by other males, either within the same summer (breeding season) or in succeeding summers. The experimental plots were searched at intervals through the summers and removal was continued as long as males could be found. For comparison, several 23-acre control plots, each 1000 by 1000 ft., were established nearby. On these, as over most of the study area, grouse were observed and, where possible, caught and banded. Observers tried to cover these areas more intensively than the areas outside the plots. Data on hours spent on these plots are given in the appendices.

The fairly distinct boundaries of the main zones of vegetation suggested a natural experiment on habitat selection. Fig. 1 shows that the four major types of vegetation came together near the field camp. Because of this the control and experimental plots were set out in pairs (stippled plots in Fig. 1). One removal plot was established in Very Open vegetation (similar to that shown in Fig. 2) and the other in Very Dense adjacent to it (as in Fig. 5). Removal of males from the contrasting areas was done to test habitat preferences of incoming males as well as to test the effect of resident males on other birds. The main pair of control plots was also set in contrasting habitats but here the difference was not so striking since one was in Dense vegetation (as shown in Fig. 4) and the other in Open (as in Fig. 3). In areas where searching was known to have been thorough some extra control plots were established for comparison of numbers (clear plots shown on Fig. 1). Eight of these were used, three in Very Open, two in Open, two in Dense, and one in Very Dense.

For each year, all observations of males were mapped, the scales being 1 in. to 200 ft. for study plots and 1 in. to 500 ft. for other areas. Some maps were made of observations on females as well, and all maps were used for analyses on dispersion, as shown later. The sites used by some 80 resident males were described in detail and, for comparison, similar descriptions were made for a series of points chosen randomly over the study area. Bendell's (1954) work suggested that the areas used by resident males should be searched in succeeding years to give information on death rate and replacement. and this was done for all banded males that used an area consistently over a summer. Some other methods were employed and, where these are relevant to the problem of dispersion, they will be mentioned in the next section on Results.

Fieldwork was carried out by a number of workers during the summers of 1959 (May 16 - August 31), 1960 (March 15 - August 30), 1961 (May 1 - August 31, September 4 - 7), and 1962 (March 24 - 28, April 15 - 18, May 1 - September 7). I worked on the area during the summers of 1961 and 1962, and paid special attention to the removal experiment and other studies of dispersion in 1962.

RESULTS

Interaction between males on control areas

Results from experimental work will mean little unless the pattern of dispersion under normal conditions has been examined. Therefore, this section discusses the spacing of males on the control plots and other areas away from the removal plots. After analyzing the spacing mathematically, I consider the year-to-year use of plots by males, the size of area used, replacement on vacated areas, and the differences in numbers and behaviour of adult and yearling males on control areas.

Those males that hooted and displayed on a specific area showed a tendency toward uniform spacing. This was determined by measuring nearest-neighbour distances for the resident males found over most of the area shown in Fig. 1 in 1962, excluding the experimental plots. In an area of 936 acres the minimum number of resident males was estimated from the map to be 157. By the method of Clark and Evans (1954) the mean nearest-neighbour distance for an infinitely large and random population of this density was calculated to be 255 ft. The actual mean from map measurements was 381 ft. and, when this was divided by the theoretical mean, an index of departure from randomness (R) of 1.49 was obtained. This indicates a trend to uniformity since a random population would give a figure of 1.00 and a uniformly spaced population would give a figure of about 2.15. Clark and Evans formula for testing the significance of R was used and showed that the difference from randomness was highly significant.

The type of distribution was also checked by comparison with a set of random points. On the 1962 map 157 random points were established and the distance from each of these to the nearest resident male was measured.

Ten of these distances were less than 100 ft. and 43 were less than 200 ft. None of the male-male distances were less than 100 ft. and only 16 were less than 200 ft. The average distance was 344 ft. as against 381 for the males. The two figures differ significantly at the 5% level by Chi-square. If the measurements are grouped by 50 ft. intervals (0-50', 51-100', etc.) and compared, the difference (shown by sum of Chi-square) becomes even more significant, showing that males were definitely further apart than random spacing would allow.

The near-uniform spacing was caused by territorial behaviour on the part of most of the males. Fig. 7 shows how the main control plots were used by adult and yearling males over the four summers. Some males were not banded and some sightings were not long enough for band combinations to be checked so that much time was given to cross-checking times of observations, etc., to allow observations to be assigned to a particular male. Points of observations were then joined so as to give a maximum area for each male.

The maps show only three points where territories seemed to overlap. In 1959 adult No. 17 was found near adult No. 14 on June 1 but No. 17 was silent and showed no signs of displaying when seen. The territories of Nos. 26 and 210 touch on the 1960 map but the observations leading to this were made on separate days. The same applies to the case involving No. 131 in 1962.

Territory sizes ranged from 0.2 to 9.2 acres (average 2.6) but many of these were based on only a few observations. If areas mapped from less than ten observations are omitted the average becomes 3.7 acres (range 2.3 to 6.5). Males showed no tendency to hold territories of constant size from year to year. Only one case is based on more than ten observations

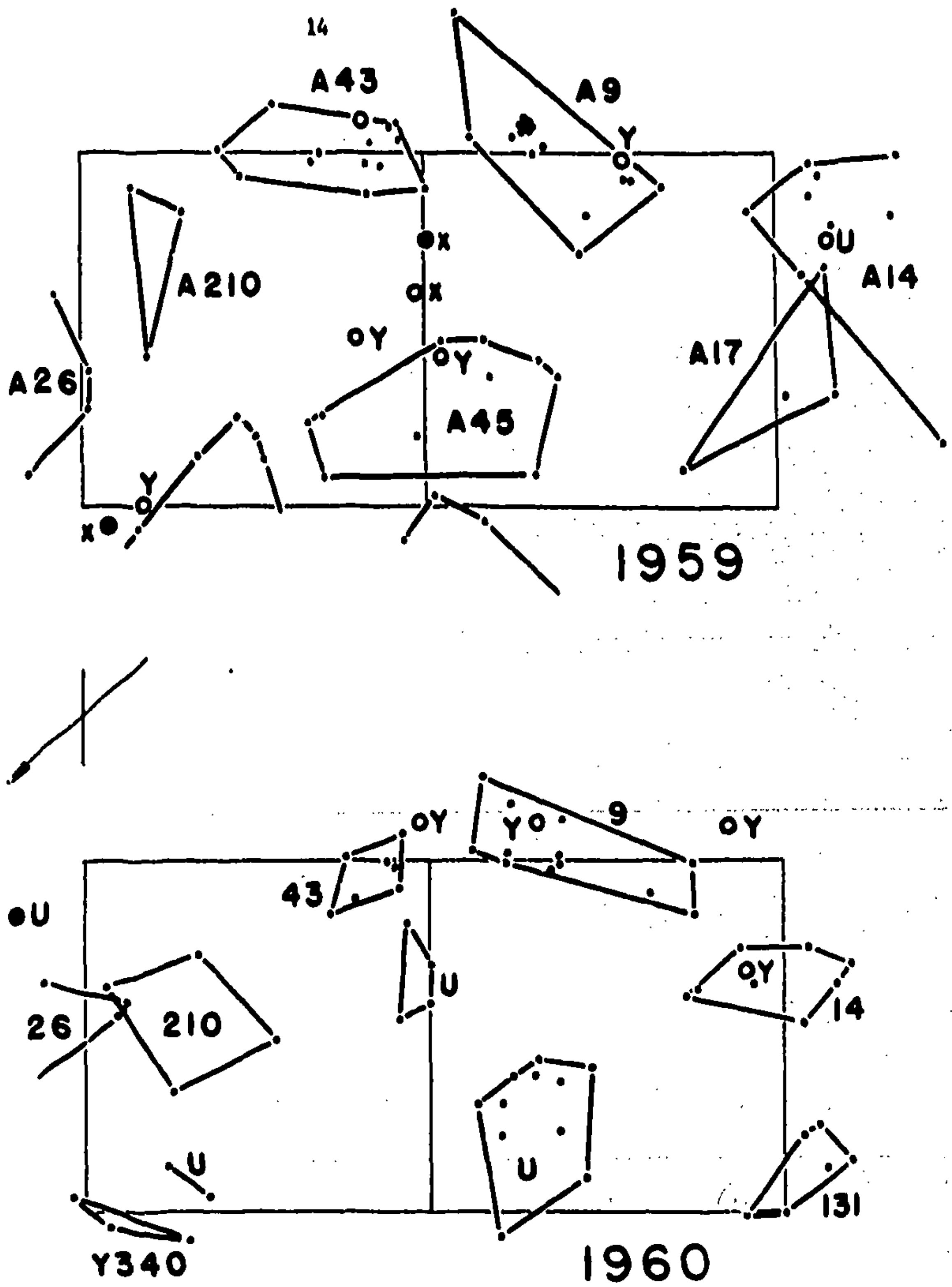
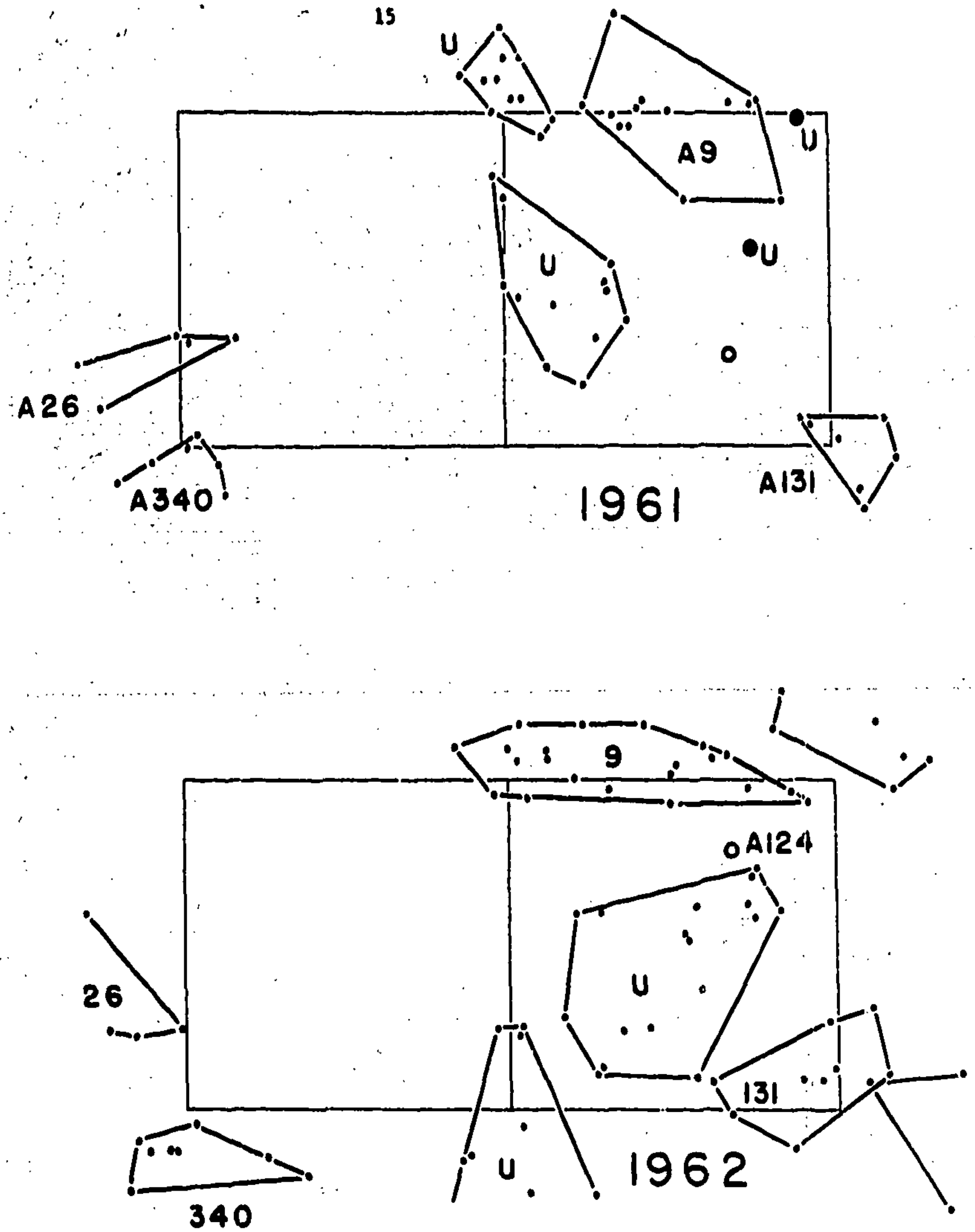


Figure 2. Areas used by males on main control plots. The left plot was in Dense habitat, the right mostly in Open habitat. Scale 1" = 440'.

Ages and numbers are given for banded males (A - adult, Y - yearling). Circles show single observations (open-silent male, closed-hooting). Dots show observations on resident males.

x - adult accidentally killed.
U - unbanded.


U
A9
U
U
U
A26
A340
1961
A131
9
A124
U
26
131
340
U
1962

every year. This male, No. 9, showed territories of 3.7, 2.6, 4.5, and 4.4 acres over the four years, suggesting that some constancy might have been uncovered with increased numbers of observations. Unfortunately the sizes correlated better with the number of observations than they did with the year or ages of the males, as the graph below shows (Fig. 8). The spread of points is sufficient that dividing each size by the number of observations used to make it does not give any more usable figures. The largest territory was based on only a few observations (male No. 14 in 1959). Late in the summer No. 14 was twice observed away from the open plot near females which he had probably pursued. Omitting these two sightings gives an acreage close to that used by No. 14 in 1960.

As expected from Bendell's (1954) work, males "homed", or showed a very close return, to their territories once these were established. Fig. 7 shows this, and it was equally true for all males banded on territory over the study area. Known banded males were seldom found away from their territories, and, if they were, the males were always silent. The observations made on males away from their territories came late in the summer (past mid-July) or, rarely, very early in the summer (early April). In all cases the unusual locations of males could be explained by assuming that they were migrating to or from the winter range.

Slight shifts in territorial boundaries were fairly common, as shown on Fig. 7. For example, No. 9 expanded his territory with the loss of his neighbours in 1962. The unbanded males in the centre of the plots shifted their locations slightly from year to year. Some adjustment of boundaries probably took place after the removal of three males from the plots in 1959, although none of these three positions were actually overtaken by neighbours in that year. These and other examples show that males would adjust their

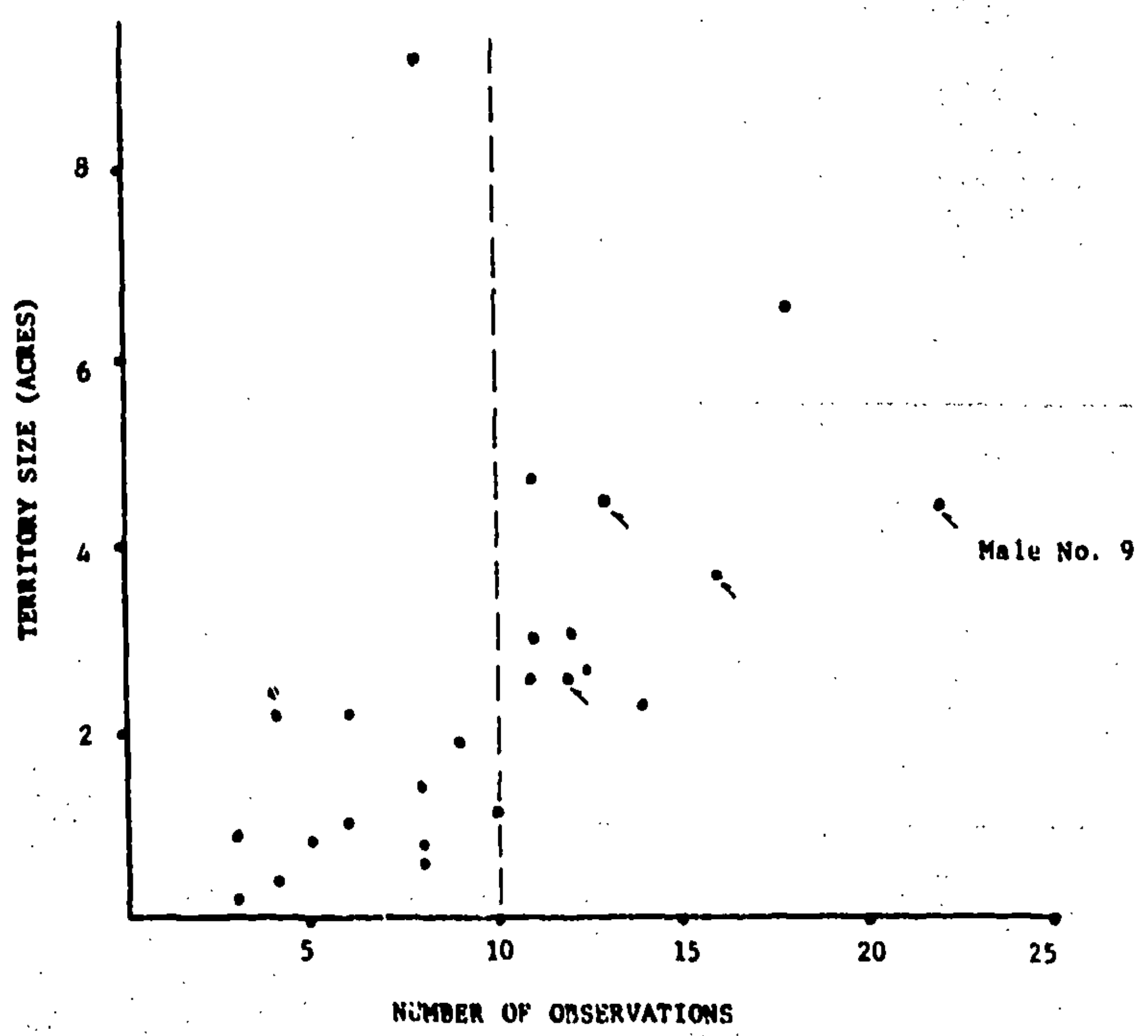


Figure 8. Graph showing relationship between size of territory and number of observations.

territorial boundaries as the positions of their neighbours changed.

Fig. 7 also shows, however, that most of the observations on well-known males were distinctly within the territorial boundaries. This suggests that, over most of the breeding season, males were not patrolling the boundaries of their territories or actively defending them. Direct fighting between neighbouring males was practically never seen. Over two summers I observed only one such encounter and that took place on a removal plot. It appeared that males knew the boundaries of their neighbours' territories since, for example, the areas used by three adults killed on the main control plots in 1959 were left vacant for the rest of that summer. On these plots neighbouring males were often seen or heard hooting quite near each other, but contact between hooting males was never observed. These points suggest two possible mechanisms that might lead to the observed spacing between territories.

One mechanism would be a short intense period of boundary adjustment through aggression immediately after males descended to the summer breeding range. This is an unlikely possibility for several reasons. In 1960, observation was started on the study area before males arrived and no unusual fighting or shuffling of areas was seen. As mentioned, males, after establishing territories, return to these in succeeding summer regardless of the number or location of neighbours. A near-uniform distribution produced by strong aggression might be expected to lead to equal use of all parts of the area but many areas of apparently suitable habitat were never used as territories.

It is more likely that the hooting and other sounds produced by a territorial male, localized around one or more favoured display spots, advertised his presence and kept other territory-holders at some minimum distance away. This mechanism allows for the possible formation of loose groups of vocal males, mentioned below. Using this idea it is much easier to account for little fighting, unused habitat, and precise homing by males.

Although mathematical analysis showed males to be spaced somewhat uniformly, field observations suggested that males sometimes formed loosely-knit groups while hooting or displaying. This is not contradictory since the mathematical treatment depended on measurement from the estimated centres of territories. These groups could have been formed by neighbouring males that were within their territories provided they approached each other as closely as the boundaries would allow. As mentioned, direct contacts between males were very rarely seen. However, actual measurements of distances between neighbouring hooting males were made for some forty cases and the distances averaged considerably less than the 381 ft. mentioned in the mathematical analyses. In all areas there was a good deal of synchronization of hooting but within these "groups" hooting seemed to go on longer and be more communal than observed for more isolated males. Evidence presented later suggests that such groups were often associated with particular types of cover and landform.

When considering interaction it is important to establish whether or not all males were able to establish territories. No non-territorial adults were found on the control plots although one of the three adults killed accidentally in 1959 was silent when collected and may not have been on territory. Banded adult No. 124 was seen on the open plot early in 1962 (Fig. 7) but he was apparently still migrating from the winter range since he was found later in the summer back on his former territory some distance from the plots. This is one of the rare examples, mentioned above, of a male off his territory early in the summer. Two other silent males on the plots may have been yearlings or residents that were not identified. Observations over all control areas suggested that there were few, if any, adult males not holding territory.

This suggestion was strengthened by a simple analysis of replacement in those territory-holders that died or were collected. Once it was clear that males homed precisely to their territories in successive summers, males that failed to show this return were assumed to have died. Forty-four of these "emptied" territories (including some where banded males were collected) were examined in the following summer. Newly adult males used the vacant areas in 20 cases, neighbouring males expanded their territories to include part of the vacant area in 11 cases, and 13 areas were apparently left vacant. Twenty-four other territories, emptied by shooting, can be used here to increase the sample size since the collecting was done in areas that were searched regularly. In this group 9 cases of replacement were discovered in the summer following that of removal. In the combined group the fraction showing replacement in the following summer was 43%.

I compared this figure with that given by a group of males that were collected from well-studied areas early in the summers. Twenty-seven emptied territories were examined and five of them were used by another male within the summer, giving a replacement rate of about 18%. One of the five was an adult and some of the others may have been. However, experimental results, given below, suggest that some of the other four males may have been yearlings. The rate of replacement by adults within a summer may then have been less than 18%. The analysis suggests that, although emptied territories were often used by other males, the replacement seldom took place until the summer following the death of the occupant.

More than two-thirds of the yearling males banded or collected outside the experimental plots showed no signs of hooting or other territorial behaviour (32 of 46 males). This includes eight yearlings banded on the control plots. Of these, two were located well within an adult's territory while two were on the edges of territories and four were outside. This might suggest that yearlings were attracted to territorial males or their territories since these covered only one-third of the area of the two plots. However, because of attraction to hooting males and delay involved in observing and banding, observers probably spent more than one-third of their time within territories while on the control plots. Male No. 131, who established territory near the west corner of the plots in 1960, was banded as a yearling on the edge of male No. 45's territory in 1959. He shifted just over 1000 feet and made use of an area that had no residents on it in 1960. None of the other seven yearlings returned to the control plots but several showed up in later seasons on the experimental plots or near the plot area. Later evidence suggests that silent yearlings do in fact frequent the territories of adults.

A few yearling males held territories and showed behaviour similar to that of territorial adults. These were three males banded outside of the plots, male No. 340 near the north corner of the control plots, and several more males that were assumed to be territorial since they were hooting when collected. The banded yearlings were observed to hoot and display to females in typical adult fashion. Three of the four returned to their yearling territories when they were adults (on Fig. 7, notice position of No. 340 over three summers). Dates of last observation suggest that the territorial yearlings may have left the breeding range before the territorial adults.

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To better understand interaction between males it would be useful to know what fraction of the males on the breeding range were yearlings and how many of these yearlings were territorial. This would allow comparisons with ratios from the experimental plots and other studies. These figures are difficult to estimate since it was much easier to locate hooting males on the summer range than silent ones. A rough method of calculation can be used which depends on the assumption that all territorial males hooted for approximately equal amounts of time (Bendell, J. F., pers. comm.). The assumption should be valid for adults but may be in error for yearlings since there was some evidence to suggest that yearlings hooted less often and with less volume than adults.

During the months of March through June, 1959-1962, 158 sightings were made of males that were definitely adult. Of these, 126 (80%) were hooting when the observation or collection was made. Using the above assumption, it follows that hooting adults were four times easier to locate than silent adults. As mentioned earlier, 14 of 46 known yearlings were hooting when observed or collected. If all hooting males are "converted" to the silent category by dividing by four, the fraction of yearlings in the whole group is 36 in 100, or 36%. By the same scheme the fraction of the yearling males holding territory would be roughly 10%.

To summarize, interaction between males had a considerable effect on their spacing at this fairly low density (about 0.15 males per acre). All the adult males and a fraction, possibly one-tenth, of the yearling males were considered to be territorial and this group showed a near-uniform type of dispersion. Territories were variable in size and showed no obvious change in size with age or year. Once territories were established the owners used the same area in succeeding summers except for minor boundary changes related to number and closeness of neighbours. Non-territorial yearlings may have been attracted to territories on their displaying owners. Several of these conclusions or suggestions are confirmed by experimental results in the next section.

<u>Interaction between males on removal plots</u>

Analyzing data from the experimental plots shows how males shot from their territories were replaced by other males. Again, it is important to distinguish two types of replacement - that occurring within the summer (breeding season) of removal and that occurring in a subsequent season. Once the two types of replacement have been examined, another section will compare results from control and experimental areas.

Over four summers, 32 adult and 25 yearling males were taken from on or very near the two removal plots. A few others were collected further away from the plot boundaries. Fig. 1 shows that the zone of Very Open vegetation extended on to the Very Dense removal plot along the common boundary of the two plots. Fortunately, the area involved was approximately equal the area of the large swamp on the Very Open plot (where no males were ever taken). Therefore, in the table below, the "open" figures include any males found in the strip on the Very Dense plot. The 46-acre size of the dense removal plot was preserved by extending its boundaries slightly to the northwest, into an area of similar vegetation. As it happened, males were usually removed from the latter strip when found since observers had difficulty seeing boundary markers along the northwest line of the dense plot and tended to collected when they had the chance. Table II splits the 57 collected males by year and activity when taken. A few adults, collected very late in the summers, were assumed to be migrants and omitted from the table.

Table II. Males found on removal plots, 1959-1962. Boundaries of the plots were modified slightly for this table (see explanation above).

	Adults		Hooting yearlings		Silent yearlings	
	Open	Dense	Open	Dense	Open	Dense
1959	4 a	5	1	0	3	0
1960	9 a, c	5 a, b	8 b	0	3	0
1961	2	0	2	0	1	0
1962	6	1 a	4	0	2	1
TOTAL	21	11	15	0	9	1

Symbols: a - one wounded, not recovered, assumed to be adult resident

b - one observed, not collected

c - two observed, not collected

After 1960, a drop in numbers of adults was evident for the Very

[illegible]

control plots (discussed in a later section on habitat selection). The lack of yearlings on the dense area is far more striking than it was on the main control plots. Since these lowered numbers were apparently a result of habitat selection, most of the discussion of interaction between males will centre on the open removal plot.

It is clear that no great influx of adults occurred on the open plot after removal of residents since the average number of adult males per 23 acres per year was 2.6 here as compared with 3.4 on all the control plots, excluding the very dense (figures for control plots given later). Cases involving replacement of an adult by another adult were rare, as shown below. More commonly, adults were replaced by yearlings. Table III shows that 60% of the yearlings were hooting when taken from the removal area. This percentage is almost twice that found in control areas, suggesting that more yearlings would attempt to hold territory on an area cleared of adults.

One way to examine interaction in a removal experiment is to consider removal and repopulation on certain favoured areas. I outlined such areas as objectively as possible within the two plots and found that all the observations and points of removal of males could be enclosed within areas that involved less than one-quarter of the area of the plots. Fig. 9 shows the areas which were defined, identified by letters.

It should be mentioned that this analysis was first done on a larger scale, using some areas which were completely outside the boundaries of the experimental plots. The shorter analysis gave results which were exactly comparable to those of the longer, and is presented here, being easier to follow.

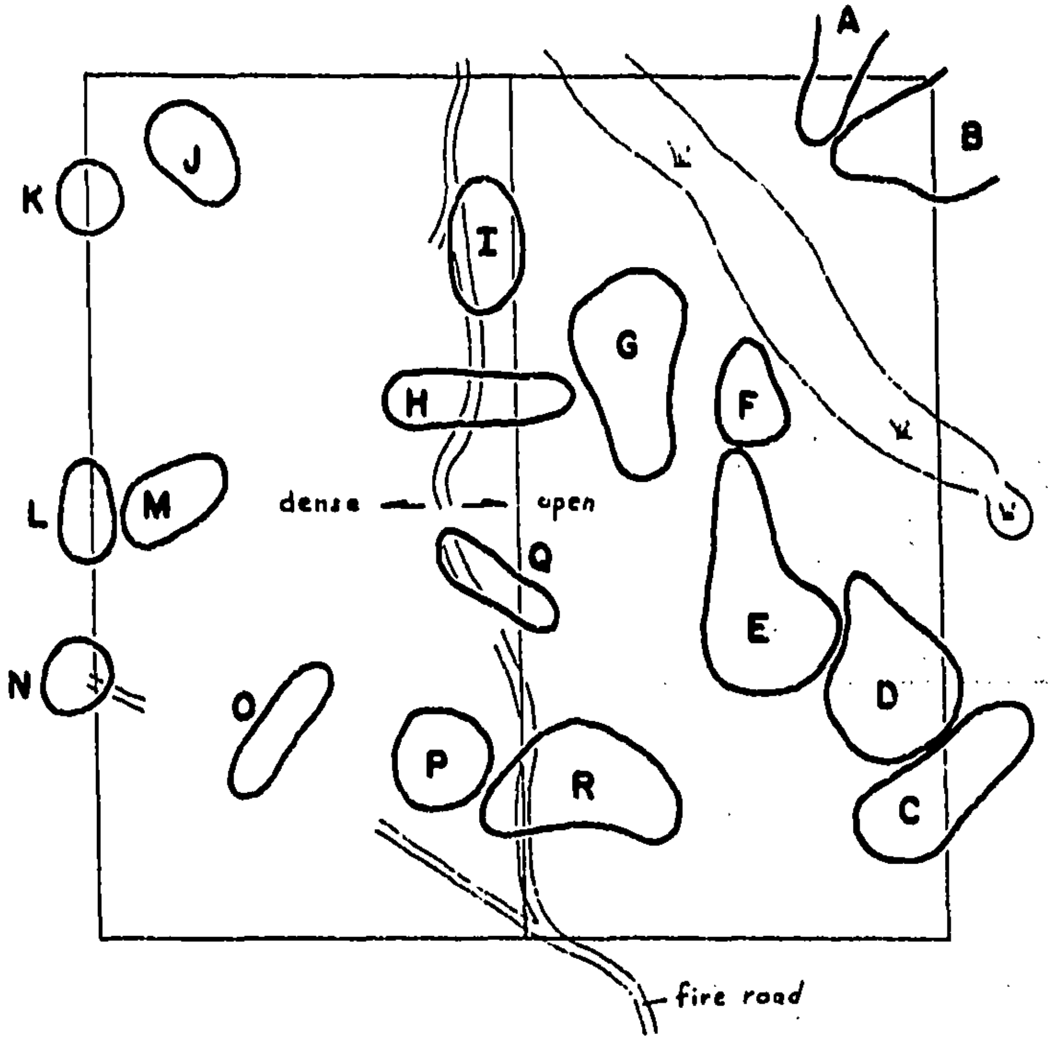


Figure 9. Favoured areas, used for analysis of removal and repopulation on experimental plots. See text and Table IV. Scale: 1" = 440'.

more than one male was removed from a given area. They are probably equivalent to territories since they occur with about the same density and spacing as the territories on the control plots. Whether or not the areas represented territories is not too important. The main point is that neighbouring males and replacing males had to be separated if this analysis was to be useful. In most cases the separation was made fairly easily by checking in fieldnotes which observations were made simultaneously and by measuring map distances between collected or observed males. In a few cases the assigning of males was difficult and errors may have been made, as suggested below. Table III, below, shows how the 18 areas were used over the four years. The table will be used in a later section on habitat selection as well as here.

Table III. Use of specific areas on the removal plots by males from 1959 to 1962. See Fig. 9 for location of areas. Time scale in each year runs from left to right. Symbols explained below.

Area	1959	1960	1961	1962
A		A		
B		h	s	h
C	A, hy	hy	A, h	A, h
D	sy, A, sy, hy, sy	A, A, hy	hy, h	A, hy, h
E	h	A, sy, hy	hy, h	A, hy
F		hy, hy	sy	
G		A, hy, hy, hy	s	sy, hy, hy
H	A	s		s
I		h*, sy	A	
J	A	A		
K		A		
L	A			
M	A	h*		
N		A		
O		h		
P	A	h		
Q		s	s	h*
R	A	sy, A	s	A, sy

Symbols showing use of areas:

A - adult (Note: a few late-occurring silent adults were assumed to be migrant and omitted. All remaining adults were considered to be territorial).

hy - hooting yearling
sy - silent yearling
h - hooting male, not collected or identified
s - silent male, not collected or identified
* - wounded, not recovered

During the experiment, there were 19 cases in which an area was used by only one hooting male during a given season (one of these hooters was known to be a yearling). In other cases only one observation on a silent male came out of an area during a summer. There were 8 such cases and again one of the males was a yearling. These figures immediately suggest that replacement was not the commonest reaction to the removal of a male. A count from Table III shows that 16 "territories" were used by more than one male and these cases are discussed in the next few paragraphs.

Over four years there were eight cases of removed adults being replaced by hooting yearlings. The intervals between collection of adult and yearling varied from four days to a month. In one case an adult was successively replaced by three hooting yearlings at intervals of four weeks, one week, and two days. A second adult was replaced by a silent yearling after five days, a hooting yearling after another four weeks, and a silent yearling after five more days. A silent yearling was also taken from the area before the adult was found. In another case a hooting adult and a hooting yearling were taken from the same area on the same day. It may be significant that another adult had been removed from close by five days earlier. Perhaps my boundaries were not realistic in this case, and the yearling was actually reacting to the vacancy created by collection of the latter adult.

Yearlings may have replaced adults in some other cases. One area used by an adult later yielded a silent yearling. Two vacated areas were used by unidentified hooting males. Another area produced a silent yearling after a hooting male had been wounded but not collected. Yearlings acting in an adult manner may have replaced removed adults in up to 13 cases (or 14, as suggested in the next paragraph).

Only one area showed use by two adults in the same summer (area D in 1960 produced a siltent adult and, three weeks later, a hooting adult). Hooting was heard on nearby area C two weeks after collection of the silent male and, eventually, a hooting yearling was collected there. The hooting or display of the silent adult may have been centred closer to C than D. This explanation is strengthened by the fact that the hooting yearling on C was the one mentioned above, the only known yearling among the group of hooters that were never replaced within a season. Since the silent adult was taken on April 12 another explanation might be that he was still migrating and had not yet settled on territory when he was collected. Just outside the open removal plot another apparent case of adult replacement was found in 1962. In this case one of the two adults collected was a banded male, whose territory from 1959 to 1961 was several hundred feet from his point of collection in 1962. The shortage of cases of adult replacement suggests that there was no surplus of adults present during the time of the experiment.

On five areas the first male to be collected was a hooting yearling. Although some of these might be explained in the manner described above, there were apparently some yearlings holding territory in adult fashion from the start of the season, just as there were on control areas. Yearlings may have found it easier to establish territory on the removal plots since they would only have to compete with new males, not residents of earlier years. Just outside the open removal plot a silent adult and a hooting yearling were taken from the same area on the same day. In this case the yearling must have been holding territory in spite of neighbouring adults.

Several of the 25 yearlings taken from the removal area, then, were apparently territorial along with the adult residents. But, what fraction of the yearlings showed territorial behaviour only after the residents were removed? This percentage can be estimated in several ways. The simplest is to consider the fraction that were hooting when collected. This would give a replacement rate of 64% (Table III). Some of these were territorial in their own right, as mentioned, and some of the silent yearlings may have been showing territorial behaviour, even though they were not hooting when collected. Therefore, I tried to estimate from Table III the maximum and minimum number of cases of replacement by yearlings.

A minimum estimate of the percentage of yearlings that became territorial only after removal of residents (adult or yearling) was 44% (11 out of 25). This figure was reached by considering only those that were hooting when collected (total 16) and assuming that, when a hooting yearling was taken first from an area, it was a territorial resident before removal (five cases). A maximum estimate was 77% (23 out of 30). This was obtained as follows: by counting all hooting yearlings but three that were taken after a resident was collected, and including five other unidentified hooters that came onto areas after residents. The latter five also had to be added to the total yearling count which then became 30. Between these two extremes the best estimate of the fraction that replaced, considering time intervals between collections and fieldnotes on hooting heard at collection times, was 62%. Thus, almost two-thirds of the yearlings on the study area would not take up territory until the resident territory-holders were removed. This figure would be higher than that representing the percentage of adults replaced by yearlings since some adults were followed by more than one yearling. Also, the three yearlings assumed to be original residents had some replacements.

One tendency mentioned in the first section is confirmed by these past few paragraphs. Many of the replacing yearlings were found on a "territory" only a few days after the resident was shot. Two silent yearlings were removed from areas which later produced a hooting resident. Only one silent yearling was collected from an area that gave no territorial male in the same summer. Yearlings were not collected on the plot outside of the areas shown in Fig. 7. All these data indicate that yearlings were found on territories much more often than chance would allow. Since yearlings collected later in the summers chose areas that were previously occupied over empty ones, the attraction was clearly to the territory-holder rather than the territory itself. These points do not apply to the few yearlings that were territorial from the start of the season. Notice also, from Table II, that these preferences are superimposed on a definite habitat preference, discussed in a later section.

It is also interesting to examine which areas were not used by males. In various years, 29 areas out of a possible 72 were not used (Table III). Most of the vacancies were related to habitat selection and this will be discussed in a later section. One point that seemed to be related to interaction was that only one vacancy occurred in 1960 while 1959, 1961, and 1962 had 9, 9, and 10. This difference must be explained and several possibilities are explored.

The most likely reason for such a low number of unoccupied territories in 1960 would be a higher density of males in that year. Fig. 10, given later, shows that, while 1960 did have possibly the highest density of males, the figures were close to those of 1961 and 1962. The number of new males was definitely higher in 1960 than in following years, and this is probably more significant in explaining the vacancies since this group was settling the removal plots. Another explanation can be proposed here, involving the times of searching on the removal plots. 1960 was the only year in which the plots were covered thoroughly in March and April (see table in appendices). Hooting males were never found on the removal plots in March but in April, when hooters were present, some emigration could have taken place. Any males that left at this time would have been collected only in 1960. It may be significant that the only direct aggression between a pair of males that I ever observed took place on the open experimental plot on April 16, 1962. The threatening and chasing may have been between an adult and a yearling however, since an adult and a hooting yearling were later collected on this area (area E, Table III and Fig. 9). An argument similar to this was rejected when the mechanism causing the observed spacing of territories was discussed earlier. The correlation between the low number of vacancies and the high number of new males in 1960 seems to be the significant one.

An explanation involving early searching in 1960 might be used to explain the lower number of males collected on the experimental plots in 1961 (Table II). Evidence given later shows that males of two years usually took up territories within half a mile of the locations they occupied as yearlings. Over the four summers, 5, 11, 3, and 7 yearlings were shot on or near the removal plots. The number was highest in 1960, probably because searching was started earlier. Some early searching was done in 1962, the year which gave the second highest number of yearlings. A suggestion emerging from this is that some yearlings may have come onto the study area and left it again before the end of April. If this is true, the higher collection in 1960 may have lowered recruitment of new adults to the same area in 1961. One of the two adults collected in 1961 was a male that was banded as a hooting yearling late in 1960 and allowed to remain on the removal plot.

The results in this section confirm some of the suggestions made in the first section. Replacement of removed adults by other adults within a given summer occurred in very few cases, if at all. About half of the removed adults were replaced by yearlings, and calculations suggest that nearly two-thirds of the yearlings on the area would only try to take up territory when residents were removed. At least 60% of the yearlings on the removal plots were hooting males as compared to one-third or less on control areas. As on the control areas, a few yearlings were apparently holding territory in the presence of adults. The number of adults removed in each year suggests that removal in one summer was not causing an abnormal influx of adults to the removal plots in the next summer. This question, however, must be decided by comparing control and experimental areas.

Comparison of control and experimental plots

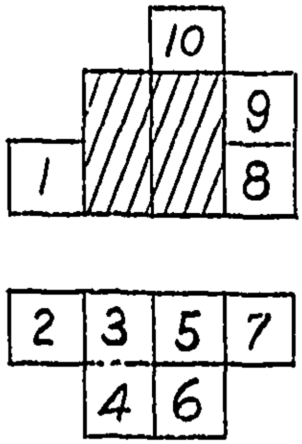
The main question to be examined here is whether the presence of resident males affected the settling of new males on a given area ("new" referring to those adults that had not held a territory in the previous year). This is best answered by comparing numbers from control and experimental plots in Very Open, Open, and Dense habitats. A rough comparison can also be made from the plots in Very Dense habitat but selection of habitat seemed to have far more effect on settlement here than interaction between males. The comparisons will involve only 1960 through 1962, since numbers of new males could not be determined for 1959.

It was quite easy to determine numbers of new males for the open experimental plot since removal was carried out in all years. The only complicating factor was a few situations involving wounded males and males that were not collected (see Table II). Once these cases had been assessed the best estimates for new males on the open removal plot (with slightly modified boundaries, as in Table II) were six in 1960. One in 1961 and six in 1962.

It was more difficult to determine the number of new males entering the control plots (estimates given in Fig. 10). Two methods were used in estimating these numbers so that they would be as accurate as possible. The more theoretical method used the total numbers for each year and the death rate of adult males. An appendix shows this calculation as well as the calculation of death rate. In some cases it was difficult to decide whether one or two males occupied a given area on the control plots. When this happened the lower figure was used so that estimates for total numbers of resident males and for new males are minimal. By this method the numbers of new males were 18 for 1960, 10 for 1961, and 10 for 1962 (38 in all, excluding the Very Dense plot). In the second method, new males were reckoned from map positions, the method being made more accurate by the presence of many banded males among the unmarked ones. This estimate gave 18, 12, and 14 new males for the three years and the total of 44 was probably more accurate than the total of 38 from the first method.

The numbers of new males shown in Fig. 10 are those determined by the second method. If sub-totals are extracted, it becomes clear that the proportion of new males was higher for the control plots in Very Open than it was for those in Open or Dense habitats. On the Very Open plots 59% of the

Figure 10. Total numbers of resident males found on control plots over four summers. After 1959, an estimate of the number of males that were new to each habitat is given in brackets for each total.



Nos. 3 and 5 were the original (main) control plots.

// Removal plots

Plots (refer to sketch)	1959	1960	1961	1962	M/P/yr	NM/P
No. 1 (Very Dense habitat)	1	4 (3)	1 (0)	0	1.5	3.0
Nos. 2, 3, 4, (Dense hab.)	8	12 (6)	12 (5)	9 (2)	3.4	4.3
Nos. 5, 6, 7, (Open hab.)	8	11 (5)	14 (4)	11 (5)	3.7	4.7
Nos. 8, 9, 10, (Very Open hab.)	8	9 (7)	7 (3)	13 (7)	3.1	5.7
Totals for years (new each year)	25	36 (21)	34 (12)	33 (14)		

M/P/yr - Males per plot per year
NM/P - New males per plot, total for three years

males were "new" while only 39% were new on the six control plots in Dense and Open habitats. This suggests that, when the comparison between numbers of new males on control and experimental areas is made, only control plots in Very Open habitat should be used. This comparison is made below and the experimental plot is also compared with all the control plots taken together, excepting the single one in Very Dense vegetation.

Table IV. Comparison of numbers of new males on control and experimental plots. The figures indicate new males <u>per plot</u> (23 acres).

	Control plots		Experimental plot
	Nine plots in V.O., O., and D. habitat	Three plots in V.O. habitat	Large plot in V.O. habitat
1960	2.0	2.3	3.0
1961	1.3	1.0	0.5
1962	1.6	2.3	3.0
TOTAL	4.9	5.7	6.5

None of the comparisons using the figures for new males give significant differences when Chi-square tests are applied (using a 5% level of significance). This statement holds for all comparisons between control and experimental plots, whether total figures are compared or Chi-square values for each year are summed and compared. Apparently, new males made approximately equal use of emptied plots and plots having residents when they first took up territory. During 1960 - 1962, then, the presence of resident males had no significant effect on immigration of new males.

This condition even held for the plots in Very Dense habitat. A rough comparison shows that, from 1960 through 1962, six adults were taken from the 46-acre removal area in Very Dense vegetation (Table II) and three new males were estimated to be present on the 23-acre control area in similar habitat. As mentioned, habitat selection was probably more important here than interaction judging by the lack of residents after 1960.

The next two sections will examine the effect of this selection on the dispersion of the males.

One further comparison, concerning the behaviour of yearlings, might be drawn in this section. On control areas, it was estimated that roughly 10% of the yearlings were territorial. This would have been perhaps three or four percent of all the territorial males. On the open removal plot over 60% of the yearlings were hooting when collected. The difference, 50% or more, is the fraction that was presumably prevented from establishing territory by the residents. This figure is quite close to the 62% figure estimated from the analysis of Table III. Notice also that the number of yearling males holding territory on the open plot before shooting may have been higher than three or four percent, perhaps as high as 12% (three yearlings in a total of 21 adults and three yearlings). If this is true, the two estimates agree very well and indicate that just over half of the non-territorial yearlings would hoot and display only after residents were removed.

These comparative results have been presented in a separate section since they are basic in determining what effect interaction had on the regulation of breeding numbers of males. There was no detectable surplus of adult males as uncovered in other avian species by Stewart and Aldrich (1951), Jenkins (1963), or Choate (1963). The yearling males that replaced collected adults might be considered surplus but results from other sections show that the yearling's rate of death was not noticeably higher than that of the adults. Simard's (1965) work indicates that, although yearlings were capable of fertilizing hens, they matured later and showed a lower level of testicular development than adults. A very low level of interaction may have served to prevent this group from becoming territorial. These yearlings, while they did not contribute to the uniform pattern of spacing and likely did not mate with females, showed no ill effects from their interaction with other males.

<u>Habitat selection by males on control areas</u>

This section tries to answer the question "What sort of habitat is preferred by males for their territorial and other activities?" It was clear from observation in the field that males used certain types of habitat more frequently than others when hooting and displaying. On a larger scale, when the vegetation and topography of territories were examined, preferences could again be seen. This selection likely had an effect on dispersion as great as interaction, perhaps greater at some ages. The following paragraphs, therefore, examine these preferences and also provide background for the next section which will examine preferences in the absence of interaction.

For this and the next section there is an important preliminary point. The density of vegetation was apparently increasing quite rapidly on some parts of the study area during the four years. An example to show this comes from Table I. Notice that Very Open and Open habitat differed mainly in the amount of coniferous cover (2% versus 28%). Other factors being equal, this must have been caused by the differences in time of Douglas fir planting. The Very Open was planted about five years after the Open and thus the 26% difference in cover developed over this short time. Comparing 1962 measurements of vegetation with fieldnotes describing known points on the dense removal area led to the same conclusion. The effect of these changes on the dispersion of the grouse, especially in dense areas, is mentioned later.

I examined the vegetation and topography of 81 territories and compared these with similar analyses done for 69 points chosen randomly over the entire study area. Since the area used for analysis (circle of about 0.18 acres) was much less than the size of the average territory, I tried to do the analyses on the area used most often by the resident for hooting and displaying. Many features of the areas were assessed and the more important comparisons are given in a table in the appendices, and discussed below.

Males apparently favoured open vegetation for their territories. Recall that more new males were found on control plots in Very Open habitat than in other types (preceding section of Results). Many more territories than random points were located in the zone of Very Open vegetation and only one territory was in Very Dense vegetation. One territory was located in an alder area while nine random points were in alder, swamp, or bog areas. Although cover by trees and shrubs was less for territories the difference was not significant (Chi-square test, 5% level). Since territories were found more often in the open, this suggests that males hooted and displayed near patches of thicker vegetation on their territories. Territorial males often centred their activities around the edges of clearings or old logging roads, especially where the vegetation in general was Dense or Very Dense. This, too, may have raised the average figure for tree and shrub cover on territories since the vegetation at road-edges was often thicker than that of surrounding areas because of water trapped by ditches or mounds of earth. This was the only choice that might be called "edge effect", or unusual use of boundaries between different habitats. The cover by ground vegetation was significantly less on territories indicating that males used areas where they could move most freely over the ground. These comparisons show that males, when first establishing territory, preferred areas with open vegetation and sparse cover at ground level, even though they used thickets or heavier patches of vegetation for cover when hooting or resting.

A comparison of topography shows that males preferred elevated areas for territories. One-quarter of all the actual sites examined were on obviously elevated positions while practically none of the random points were. In addition, many of the other territories had elevated points nearby but outside of the circle used for analysis. Likely some of these points were included within the territories of the males concerned.

Beyond the above, there was little difference in the sets of data from territories and random points. There was no evidence to suggest that particular plant species, wet areas, grit and dusting material, direction of slopes or height of trees had any effect on the location of territories. An attempt was made to judge areas for escape and roosting cover but it was very difficult to do this objectively and no differences were uncovered.

A simple comparison using the 44 "emptied" territories mentioned in the first section of the Results also shows what areas were favoured for establishment of territories by new males. The table below shows how the rate of replacement varied with type of habitat.

Table V. Comparison of vegetation at vacated territories and use of these territories in succeeding years.

Type of vegetation	Rep.	Vac.
Very Open	60%	37.5%
Open	35	12.5
Open-Dense mixture	0	12.5
Dense	5	21
Very Dense	0	12.5
Dense plus alder grove	0	4

Rep. - vacated territory occupied by new male
Vac. - vacated territory occupied by neighbouring male or left vacant

The sample sizes are not large, but it seems significant that 95% of the replacement took place in open types of vegetation. Of the areas that were left vacant or taken over by a neighbouring male, only 50% occurred in the two most open habitats. In both columns high percentages occurred in the very open category since this was the most common type over the study area.

I also compared the numbers of resident males on control plots in different types of vegetation. Fig. 10 gives the numbers for each year and, for 1960-1962, shows an estimate (in brackets) of the number that were new to the plots in the given year. The numbers of residents per control plot per year, starting with Very Open and working through Very Dense, were approximately 3.1, 3.7, 3.4, and 1.5. It would seem that all types but the Very Dense were used about equally by territorial males. Counts of hooting males were made along census lines in Very Open, Open, and Dense habitat, and the numbers of resident males here were approximately equal also. However, although the numbers are not significantly different, the estimates for new males become gradually higher as the more open plots are considered (right-hand column, Fig. 10). Another count involving some Very Dense habitat was made along old logging roads in May and June of 1961. Thirty-one hours of counting gave 4.4 "hooters per hour" for open habitats (two types combined) and 3.3 for dense habitats (Dense and Very Dense vegetation). While none of these comparisons show significant differences, they seem to reinforce the suggestion that males settled in open areas more often than would be expected by chance movements.

These preferences were probably responsible for a drop in use of some control plots by males. The main control plot in Dense vegetation (No. 3, Fig. 10) is one example. After 1959, yearling No. 340 was the only new male to establish territory on this plot and he made frequent use of the main road near the plot and areas to the north of the plot. No silent yearlings were banded on the plot after 1959 but some could have been present since, although no territories fell within the plot after 1959, there were a few observations on silent males. Hooting was heard deep within the plot at least once during this time but no new resident was located and the sound was probably made by one of the males living near the boundaries (Fig. 7). This plot had more cover by alder and swamp vegetation than did surrounding plots, and the cover probably regenerated more rapidly. There were some elevated points but the relief was less broken and the average elevation lower than the main control plot in Open habitat. The drop in recruitment was not reflected by other control plots nearby in Open and Dense vegetation.

On the control plot in Very Dense (No. 1, Fig. 10) a similar drop occurred. The next section will show that this was reflected by the adjacent removal plot. While these drops in recruitment of territorial males are very helpful in showing the effect of habitat preferences on dispersion, they are perhaps more important in showing the effect of interaction on the holding of territory. Several authors have suggested that interaction may force some members of a population to seek space for territories on unfavourable areas away from the preferred habitat (Jenkins, 1963; Kluyver and Tinbergen, 1953; Svardson, 1949). This apparently did not occur on the Middle Quinsam area. Even the yearlings that were prevented from establishing territory did not show this emigration to denser habitat, suggesting that their urge to take up territory was low. It may be concluded that the territorial behaviour of males in favourable (open) areas did not force other males into denser habitats. It follows that the use of certain habitats over others was based on preference alone.

The above paragraphs analyze habitat preferences of males by several methods; comparing territories with randomly-chosen points, examining replacement at territories in different habitats, and counting numbers of territories in different habitats. Another method is to examine the sites within the territory used for different activities, especially hooting and displaying, since territories appeared to be organized around a few such points. This was done for the main control plots, and, as expected, the favoured hooting sites were elevated points having some cover available - small thickets, small Douglas firs showing spaces between foliage and ground, tangles of logs, and spaces under logs and stumps. Displaying was apparently done near these points, on sites having little or no ground vegetation. Accumulations of droppings showed that males spent much of their time at these points.

To show further how use of cover on territories varied with the male's activities, I made a rough comparison of the positions of hooting and silent males. The silent category probably includes a few observations on silent yearlings but in this approximate comparison I judged that these would make no difference. The comparison, based on about 300 observations, is shown in Appendix 6. The types of cover had to be kept quite general since they were described by several different schemes in the fieldnotes, depending on the observer and the year. The percentages of silent and hooting males found in many types of cover were similar, suggesting that a male, given a proper stimulus, might hoot from almost any spot. Silent males, however, were seldom found in open clearings, on elevated points, or on top of logs or stumps. This suggests that males intending to hoot or display sought out these open or elevated spots. Hooting males were seldom found in low areas near streams or swamps. These were likely feeding and shelter areas and males found here might show the least tendency to hoot. The points of difference in the table verify, on a smaller scale, the preferences suggested by the earlier analyses.

Most of the groups or aggregations of males, mentioned earlier, were located in Open or Very Open vegetation, particularly along roads or near large clearings. The two best-known groups, both found in Very Open habitat, used areas which were probably optimal for the formation of such a gathering. One of the groups used an open gravel pit which was elevated around its boundaries and which contained several deciduous thickets and mounds of earth. The other group used an area at the junction of several old logging roads which was nearly bare of vegetation at the centre and had several ridges and piles of logs around the edges. In all cases the open habitat must have allowed males to see and hear each other easily while still keeping a minimum distance between the territories. On sites such as the two mentioned the communal nature of the behaviour might be accentuated if the males used the ridges and promontories for hooting and the central bare areas for displaying.

One further point concerning the dispersion of males in the Very Dense habitat should be made. The nearest-neighbour analyses of the first section in the Results involved very little of this type of habitat, which was apparently avoided by settling males. When the dispersion of the few males involved was examined using this method the spacing seemed to be closer to random. This was a predictable result which might have come about in two ways. The distribution would approach randomness if males were holding to their territories, immigration by new males was nil, and the males were dying at random (Skellam, 1952). The same trend might show if males shifted their positions so as to be near randomly-located openings in the increasingly dense vegetation. The latter was apparently responsible, at least in part, for the spacing since fieldnotes from 1959 and 1960 mentioned that males on and near the plots in Very Dense were collected or seen near clearings.

Before leaving this section, passing mention should be made of certain habitats that were virtually never used by males during the breeding season. On the study area males apparently avoided extensive swamps, extensive stands of mature alder, peat bogs, and large unbroken areas of fallen logs. The smaller and drier stands of alder, showing some grass and other vegetation at the ground level, were occasionally used by males. The stands avoided were those that had a heavy covering of litter and dead leaves on the ground. This suggests that the above areas were avoided because they lacked open areas at ground level. These negative comments on habitat selection apply equally well to females and juveniles.

To summarize, this section shows that males preferred certain spots for their territorial activities and that, ignoring the effect of interaction, these preferences led them to select certain habitats over others for the territories. The main preferences were for open vegetation and, beyond this, elevated points and patches of ground free of low vegetation. The next section will explore these preferences further using the experimental areas.

Habitat selection by males on removal plots

Several significant results on selection of habitat emerged from the removal experiment. Most of the data used here again comes from Table II and III. Evidence for habitat selection is shown first by comparing the two plots, and then by looking at positions used within the plots.

When the Very Dense and Very Open plots are compared the most striking difference is that virtually all the yearlings were found in the open. Only one of 25 yearlings was found in the Very Dense plot and this silent male was less than 200 ft. from open habitat. It is clear that the difference was not caused by attraction to adults since ten adults were taken from the dense area in 1959 and 1960, during which time no yearlings were found on the same area. Silent yearlings may have been harder to find in dense than open, and this bias might be used to explain some of the difference. However, almost one-third of the [illegible] females found on the experimental plots were in the dense half and these females were as difficult to find as the silent males. The highly significant difference must have been based on habitat preference.

This preference likely caused the drop in use of the dense removal plot by adults beyond 1960. In the last section it was mentioned that males collected or seen in Very Dense habitat were usually next to openings. Most of the fieldnotes describing this came from the removal plot in Very Dense. It appears that regeneration had closed most of these openings by 1962, although some small areas on the plot could still have been described as Dense or even Open habitat. From this and from information in the last section it appears that new adult males kept the habitat preferences they had shown as yearlings.

If the preference is as strong as suggested, why did at least three adults, and possibly five, use the area in 1960 (Table II)? Two points, mentioned earlier, may be important in explaining this. One is that the Very Dense habitat was probably much more open in 1960 than it was in 1962, when analyses of vegetation were done. Then, collecting [illegible]

May in 1959. A few yearlings could have been attracted to territorial adults on the dense plot, and left before May. These might have returned as adults and found the dense plot attractive enough to cause them to establish territories there. In 1960 searching started earlier and more yearlings were taken so that this return likely would not occur. Even if this argument is rejected, it must be remembered that the experimental procedure did not allow determination of territorial boundaries. The territories of some of the males in the dense habitat may have extended on to the open. Recall also that this drop in numbers of territorial males after 1960 was observed on the control plot in Very Dense and on one of the Dense control plots.

Another way of examining differences in use of the two areas is to consider the 29 vacancies in Table III. Of these, 19 involved territories that were in the dense area. Over four years, 37 areas were not used at all by hooting males. Of this group, 21 were in the dense plot. The number of vacancies on the open plot, then, jumps from 10 to 16 when an area is taken to be vacant unless used by at least one hooting male in a season. The corresponding increase on the dense plot is two vacancies. The difference was likely caused by a higher density of silent yearlings on the open plot. If true, this adds to the evidence for a strong preference on the part of the yearling males.

Because the two types of vegetation on the removal area were quite sharply defined along the boundary common to the two plots, the importance of "edge effect" in habitat selection by males can be tested. Four of the lettered "territories" used earlier lay across this boundary area. If the more complex analysis involving territories outside the plot boundaries (mentioned earlier but not presented) is employed the number of territories on the edge becomes five out of 23 (22%). On the five territories, five out of 28 known adults (18%) and three out of 27 known yearlings (11%) were found over the four years. The fraction of adults found on the five areas is not significantly different from what would be expected if these areas were being used randomly. The use by yearlings is significantly lower than would be expected. This might result from avoidance of dense habitat by the yearlings or from selection of more favourable territories away from the edge. The latter is discussed further in a later paragraph.

Of the territories shown in Fig. 9 only three were used by at least one hooting male in every year. These areas (C, D, E) were located on the most elevated and prominent area of the open removal plot, which was itself the most elevated part of the study area. The preference for open and elevated points, then, was as noticeable on removal plots as it was on control areas.

There is some evidence to suggest that the mentioned territories were used by more males than would be expected, even if only the open plot is considered. When territories in the open removal area only are examined, nine out of 16 known adults were found on areas C, D, and E. The expected number would be five, if all territories in the open were used equally. When known yearlings are counted, 13 out of 25 were on the three areas, and here the expected number would be between 7 and 8. The difference in numbers of adults is not quite significant while that of the yearlings is significant (Chi-square). Six of the remaining yearlings were found on area G (Fig. 9) and this was also a high and prominent area. If C, D, E, and G are considered together the use by yearlings becomes highly significant. This probably came about through a double preference by the yearlings - a tendency to stay near elevated points and near established territories.

The open part of the experimental area, considered as a whole, must have been a highly favourable area for settlement by males. This is shown by evidence just presented, and by the fact that a number of yearlings banded some distance from the open plot were collected as adults within the plot in the season following their banding. Another adult taken from the open plot had been banded as a chick near the main control plot in Open habitat. It is significant that even this attraction, based on habitat selection, was not sufficient to produce a higher than expected number of new males on the experimental area. This reinforces the earlier conclusion that resident males were not forcing new males into empty areas.

Results from control areas suggested a preference for open and elevated areas on the part of males, and analyses from removal areas confirm this. More important, the positions of males on the removal plots show that the preferences are very pronounced in the yearling males. Excluding the effects of interaction, this is probably the most important factor determining the dispersion of males, and the use of a given habitat by males. It has already been mentioned that males showed little tendency to shift their summer positions once they had established territories. Examining the movements of males prior to their taking up territory, as well as the spatial relationship between females and males, should show how important these habitat preferences are to the population as a whole.

<u>Dispersal of juveniles and movements of yearling males</u>

[illegible] wholesale shift in location of a population. Movements of territories from year to year were always small and could be classed as minor changes allowing for presence or absence of neighbours, movements involving changes in a "group" of males, or artifacts resulting from two few observations on a given male. The data given in the sections below on females show that females two years and older also exhibit a fairly close return to their locations of the previous year. It is suggested as well that females are attracted to territories in the early part of the breeding season. The use of any suitable new habitat by grouse must depend on the movements shown by birds before they become adult. With these points in mind, this section examines the dispersal of chicks and the movements of males before they become adult.

When considering dispersion and the use of habitat by grouse it is important to know whether juveniles return to the area of their birth or first few weeks of life, to an area of similar habitat only, or to an unrelated area. It is difficult to obtain large samples for such an analysis since mortality of juveniles is very high in the first few weeks. For example, out of some 250 chicks that were banded on the Middle Quinsam area, only five were recovered in later summers. This does not include some chicks that were taken by hunters in the autumn following their banding. These were omitted because the movements here involved migration to the winter range rather than dispersal over the breeding range. Of the five, only two were males and both were recovered as adults, two years after they were banded. One of the males was recovered as a silent adult on an elevated part of the open removal plot 2300 ft. from his point of banding in Dense vegetation. The other was found in Open vegetation approximately 7000 ft. from his point of banding which was in Very Open vegetation. These few data suggest that males were not returning to the areas they used as chicks or to areas of similar habitat. Also, the fact that three juvenile females were recovered as yearlings while no juvenile males were, suggests that some yearling males may not have descended to the summer range.

For drawing further conclusions about dispersal of juveniles it is convenient to lump male and female chicks into one group. When all five of the chicks mentioned are considered the average distance from point of banding to point of recovery was very close to one mile. This again suggests that chicks were not showing any "homing" behaviour. It is likely that few returned chicks were missed since one of the two males was found as a silent bird and the three females were all found in early summer [illegible]n females were harder to locate.

The next step was to estimate the number of chicks that should have appeared on the area to see if dispersal really was occurring or if the low return was caused by mortality. From banding records an approximate count was made of all those chicks that were large enough to wear adult leg-bands. In any case, none was counted that was less than 200 grams. This gave approximately 140 banded chicks that were assumed to have escaped the very high early mortality found in broods. However, I rated the mortality for this group at 50% rather than 25%, the figure suggested by results given earlier. If the between-season movements of these chicks averaged one mile, a few of them would be expected to show up outside of the area searched, when they returned. The number would not be large since most of the chicks were banded near the centre of the study area. If this fraction was 20% at the most, then about 56 juveniles should have been found on the study area as yearlings. Since some yearling males may not have appeared on the summer range, it might be better to say that an estimated [illegible] juveniles should have been found on the study area as adults (figure obtained by omitting chicks banded in 1961 and applying death rate of yearlings, discussed below). It is clear that the estimated figure is significantly higher than the number that actually returned. This holds even if the first-winter mortality is assumed to be 75%. It appears that, when chicks returned to the breeding range, they dispersed widely enough to take most of them outside the study area.

The last section showed that yearling males preferred open vegetation while on the breeding range. This was an important factor affecting dispersion and it is useful to establish how far yearlings move between their second (yearling) and third summers, and whether they show the same preference as adults. The table below presents some relevant data from nine banded yearlings. I have already indicated that a few yearlings, not included below, held territories and returned to them in adult fashion. The nine below were those recovered out of a group of 16 and it is possible that a tenth was relocated although identification was not certain. The survival of these males to age two was, then, at least 56%. The distances shown below suggest that some of the yearlings may have returned to some point outside the study area when they were adult. It is clear that the mortality rate for this group of yearling males was not significantly higher than that of the adult males, even though some of these yearlings were being prevented from establishing territory by the presence of adults.

Only one of the nine settled more than 0.5 miles from his point of banding, the average distance moved being just over 2000 ft. It appeared that some yearling males, such as numbers 34 and 466, started to localize on an area in the season before they established territory there. The preference for open vegetation shown by yearlings is apparently

Table VI. Movements of males from point of banding as yearlings (Y) to point of recovery as adults (A), with an estimation of habitat of each point.

Number	Season (Y)	Season (A)	Distance	Habitat (Y)	Habitat (A)
34	1959	1962	560 ft.	Dense	Dense
131	1959	1960	1100	Open-Dense	Open
386	1960	1961	1300	Very Open	Very Open
364	1960	1961	1200	Open	Very Open
466	1960	1961	300	Very Open	Very Open
620*	1961	1962	2500	Very Open	Very Open
638	1961	1962	1900	Very Open	Very Open
678*	1961	1962	2600	Open	Very Open
721	1961	1962	6900	Very Open	Open

Straight-line distances were measured from maps to the nearest 20 ft.

* seen three times as yearling, measurement made from last known position.

continued in the year of territory establishment. Five of the yearlings used the same type of habitat as adults (Very Open in four cases), three of them chose a more open type, and one chose a less open type. None of these observations were made in Very Dense type.

Using maps compiled from fieldnotes, I estimated the number of territorial males within an arbitrary distance (300 ft.) of the positions in Table VI. The average figures obtained from this analysis were:

1. number of males within 300 ft. of yearling (last known position) 1.6

2. number of males within 300 ft. of returned adult 0.6

3. number of males within 300 ft. of yearling (last known position), in following summer 1.4

The last figure may have been low because of inadequate searching around some points of banding in following years. However, it resembles the first figure, as would be expected. The first two figures are not significantly different by Chi-square but if a $\underline{t}$-test is performed on all the available pairs of data in these two categories there is a significant difference (paired data, $\underline{t}$ equals 2.9, $\underline{p}$ between 0.02 and 0.01). This is to be expected since the males do not usually show the effect of territorial spacing until they become adult. Note that adding one to each figure in the second category (that is, including the new adult in the count of his neighbours) would have made the first two figures equal. Also, the yearlings may have been attracted to groups of territorial males. Only one case occurred in which the banding point showed fewer neighbours than the adult location, in the same year. Possibly some yearlings, such as Nos. 34 and 466, returned to their earlier locations and then searched out an area with a lower density of territories. As mentioned earlier, No. 131 did this on the main control area. This simple analysis emphasizes the point that the spacing of territorial males was being determined by factors different from those determining the dispersion of non-territorial males.

This section shows how grouse might take advantage of a new area of favourable habitat. The few data available suggest that juvenile grouse disperse widely and show no tendency to return to the area where they were born or brooded. Males in their third summer (new adults) show varying degrees of fidelity to the areas they used in their second (yearling) summer. If the new adult held a territory as a yearling, he returned to the territory. If the new adult held no territory as a yearling, he moved anywhere from 300 ft. to over a mile from his yearling position and established territory in an area with fewer territorial neighbours than he had as a yearling. Some new adults may not have [illegible] to the summer range at all as yearlings, so that their territories would probably be selected on the basis of habitat type and presence of neighbours only. When they moved, juveniles and yearlings usually went to more open habitat than that around their previous positions.

<u>The effect of interaction on the dispersion of females and juveniles</u>

The effect of interaction on the dispersion of females was not studied experimentally. This section, then, discusses those observations that show how the positions of females were related to each other, and to the positions of males. An attempt is made to separate the observations into categories depending on whether the female was "lone", on a nest, or with a brood. Lone females can be further subdivided into pre-nesting hens, hens incubating but observed away from the nest, and hens that have lost their chicks. For some analyses it is assumed that lone hens seen before July were prehatch (mating, nest-building, incubating, etc.) and that those seen after June had lost their young.

When interaction was considered, the most important point emerging was that no evidence of any aggression between hens was ever uncovered. This can be shown in several ways, and one set of data bearing on this was obtained by mapping all the known positions of banded females. The resulting map showed that, while females did restrict their activities to a certain area over the summers, these areas were much larger than territories and overlapped a great deal. Females may still have spaced themselves by some sort of "individual distance" phenomenon but this seems unlikely judging by the observations mentioned below. It appeared that the spacing of females was dependent on habitat selection, random movements, the influence of males, or some combination of these three.

There were a number of instances in which two or more females were seen together. Several pairs of hens were seen together in the interval before incubation, two pairs were seen together during the time of nesting (assumed to be last three weeks in June), and several pairs were seen together after June. In some cases broods which appeared to have chicks of only one age were found together with two or more hens. Usually, in these cases, only one hen would respond strongly to the calls of the chicks. One brood was found with three hens, two of which behaved in a "broody" manner when chicks gave distress calls. Broods were often seen to intermingle on the range and some broods contained chicks of obviously different ages. All these points strengthen the conclusion that hens were not antagonistic toward other members of the population.

The fact that hens stayed with their chicks from the time of hatch to the time of upward migration has an obvious effect on dispersion. The broods can be pictured as aggregations of juveniles around a female, which move at random with respect to each other and become looser with increasing age of the juveniles. The location of broods was probably influenced mainly by habitat selection, as suggested later. On this study area the family groups apparently remained together at least until migration started.

There was no evidence of any permanent or even yearly pairing between males and females in this population. Males tried to court any hen that came within their view or hearing. The home ranges of hens were much larger than the territories of males and usually encompassed several territories. Banded hens were often seen near different territories at different times. However, there was some evidence to suggest that hens localized their activities near one or two territorial males before the time of nest-building and egg-laying. The influence of this preference may have carried over and caused more nests to be built on territories than chance would allow. In any case, this attraction must be discussed since it has an obvious effect on dispersion of females in the early part of the breeding season.

The positions of females on the plots were mapped and this allowed a comparison of female and male locations. Since the area covered by territories was known, the expected and actual numbers of females occurring within territories could be compared. It was observed that more pre-hatch females than expected occurred on the territories. This may have been due to a search bias, of the type mentioned earlier, but it was also found that broods occurred on the territories about as often as the measurements of areas would suggest. If no bias is involved, then pre-hatch females sought territories while hens with broods moved at random with respect to territories. It is just possible that bias was involved despite the difference since observation of males was emphazized in the first half of the summers and random searching was stressed in late July, August, and September. Another method can be used to show this preference.

It is possible to compare numbers of females on control and experimental areas, even though the plots were of different sizes, and different amounts of time were spent searching them. Table VII, below, shows this comparison. If the corrected percentages are examined, it is clear that a significantly higher number of pre-hatch females were found on the control and experimental areas. Fewer broods were found on the Very Dense area, suggesting that habitat selection was influencing the positions of broods rather than the presence of males. Broods could still have been attracted to territories by the vegetation and topography of the territories but pre-hatch hens were obviously attracted to the males on the territories.

Table VII. Number of females sighted on removal plots and main control plots, as compared to type of vegetation and presence of males.

	Removal plots		Control plots	
	Very Open veg. (36% of area of four plots)	Very Dense (31%)	Open veg. (15%)	Dense veg. (18%)
Pre-hatch females	16	5	22	9
Broods	20	2	11	5
Hours of search on area	90	31	102	53
% of pre-hatch hens*	14%	15%	43%	28%
% of broods*	30%	10%	35%	25%

* These figures have been corrected for both time and percent of area covered by given type of vegetation. The number of observations was divided by the no. of hours spent on the given area and by the percentage of the total represented by the given area. The resulting figures were converted to percentages.

Some other observations and measurements show the relationship between the positions of females and males. Hens were often found within a few feet of males, especially in the period from mid-April to mid-May. In some cases the males were banded and were seen near their usual hooting posts, suggesting that the females sought out the males. On a few occasions, two females were found within a few feet of the same male. Outside of this month-long interval it appeared that females were not seeking males as actively. Females were found near males in [illegible] interval but often the male was away from his usual centre of activity, suggesting that he had chased the female. Males often displayed to or chased after broody females but in all such cases the female showed no attraction to the male and, in some cases, the female moved away from the male.

Straight-line measurements of the movements of banded females within a given summer give some information on the attraction of females to males (about 70 measurements used). If the distances are plotted against number of days elapsed, some "rates" can be calculated from the slope of fitted lines. Lone females show a rate of movement of 18 feet/day, compared to 54 ft./day for broods. If some of the broods had started to migrate, the rate for them would make the average too high. Even with this possible bias, it seemed that lone females were restricting their activities to a much smaller area. This is probably another illustration of their attraction to males. A rate of 78 ft./day was obtained for hens that had lost their broods after June, suggesting that these females may start to migrate after they lose their chicks.

Sightings of banded females indicate that lone hens do not localize their activities around the same male(s) each summer. Straight-line measurements from the final point of observation in one summer to the next sighting in another summer show that the homing tendency is not nearly as strong in females as it is in territorial males. The distances involved are closer to those of yearling males, travelling between their second and third summers. The average for about 40 measurements was 1580 ft. and there was no obvious individual or seasonal variation. A rough calculation suggests that females might have had a home range of 30-40 acres on the breeding area over the years while the best-known males held territories of about four acres, on the average.

From these results, it appears that interaction had no effect on the spacing of females with respect to each other whether the females were pre-hatch or with broods. A positive attraction was obviously involved in the dispersion of single broods around their hen. No evidence of pair-bonding was uncovered. However, prior to hatching, females seemed to be attracted to males on their territories, and nests may also have been on territories more often than random placement would allow. If this was a true preference, then the spacing and preferences of males would eventually determine the dispersion of the whole population in any gradual movement out of an unfavourable area or into a favourable one.

The effect of habitat selection on the dispersion of females and juveniles

The preceding section showed how the location of females prior to the hatch was influenced by the location of territories. Apparently, interaction had little effect on the location of females or broods apart from this. These data suggest that the distribution of females and chicks, if it has a non-random basis, must be determined by habitat preferences. These preferences are examined in this last section of the Results.

The best data for showing a selection of habitat is the type given in Table VII. The corrected percentages indicated that broods were found using Very Open, Open, and Dense types of vegetation in roughly equal numbers, with the Open type showing slightly more use. The broods apparently avoided Very Dense vegetation. Similarly, pre-hatch females used open vegetation significantly more than dense (57 versus 43%). Fieldnotes suggested that, as with males, a number of the lone females and broods found on the dense plots were in or beside clearings. It can be tentatively concluded that females prefer open habitats over denser ones for most of the breeding season. There were not sufficient data to test the locations of nests or females that lost their broods, in this way.

The remaining paragraphs will present descriptions and comparisons based directly on fieldnotes and analyses of vegetation. Where comparisons are drawn using the four main types of habitat, it must be kept in mind that these did not occur equally over the study area. The observations used below fell, with a few exceptions, within an area that could be split as follows (omitting any minor types of habitat). Very roughly, 40% of the area was covered by Very Open vegetation, 25% by Open, 25% by Dense, and 10% by Very Dense. The paragraphs discuss the positions of lone females, nests, incubating females, and, finally, broods.

The positions used by lone females, whether pre- or post-hatch, seemed to be much the same as those used by silent males. Apart from the choice of open vegetation, the only preference that may have affected their dispersion was an apparent choice of moist areas - stream-edges, sloughs, sedge areas, or mere depressions with damp soil and above-average cover by ground vegetation. About half the pre-hatch, and 40% of the post-hatch females that were found alone occurred within a few feet of such areas. Some 80 measurements done in the field showed that lone females were found, on the average, somewhat less than 100 ft. from such places. The same measurement was made for 68 random points (those used in the section describing territories) and the average distance here was 130 ft. It appeared that lone females favoured moist areas, especially within open habitat, either for plant food found there, the shade offered, or the cover made available.

Data were obtained from 31 nests and, again, open vegetation was favoured. Of 29 nests properly described, 27 were in Open or Very Open habitat and the other two were in Dense. The 27 were split about equally between the two open types, suggesting that the Open was favoured since it covered less of the study area. The small table below suggests why Open might be preferred over Very Open for nest-sites.

Table VIII. Comparison of cover at nest-sites with cover in Very Open and Open habitats (from quadrats described earlier).

Factor being compared	Nest area	Habitat type (Open)	Habitat type (Very Open)
Coniferous cover	21%	31%	3%
Deciduous cover	20	15	12
Ground vegetation	42	20	21
Bare ground and rocks	26	17	24
"Duff"	49	73	68
Logs and stumps	18	12	12

The comparisons suggest that, once within open areas, hens located their nests in sites with better cover than random placement would give. The significant figure is probably that for cover by ground vegetation. It is also interesting that cover by logs and stumps was higher, and cover by "duff" (dead plants, moss, litter) was lower than would be expected. The actual positions of the nests bear out these points. Eleven of the nests were under logs, three others were beside fallen logs, and several were within clumps of salal or bracken. Nests were often under the canopy of a conifer, where these were available, and the degree of overhead cover was very high (87% average for 16 measurements). Nest positions showed no obvious relation to water or slope, nest material was available everywhere, and logs and roots with spaces underneath were abundant. All these points suggest that there was no shortage of sites for nests in the open areas.

The only data which can be given for incubating females is that obtained from the locations of "clocker droppings" passed by the hens while they were off their nests (described by Bendell, 1954). The positions of these show where incubating hens were feeding, watering, and dusting. A few observations indicate that these droppings may also be passed during the first few days of brooding.

About half of some 50 droppings were found beside or in wet areas and on sites having especially heavy cover by grass and herbaceous species. The sites included Carex patches, creek and beaver pond edges, and other moist areas with ground cover. A few were found near dustbaths which were generally in patches of sand, dry earth, or powdery dead wood. A few others were found on stumps and may have been left either by hens flying by stages to their feeding areas or by hens shepherding very young chicks. Almost all the others were found on old logging grades and fire roads. It was obviously easier to find droppings here but it seemed significant that the roads used most frequently were invariably those showing a good cover by Trifolium spp., Hypochaeris radicata, Fragaria spp., or similar plants. Incubating hens, then, seemed to make use of areas with especially heavy ground vegetation while they were off their nests.

Large quantities of data were obtained on broods since these were easier to find than lone females. Again, a preference for open vegetation was apparent. The most useful data were collected in 1962 when components of cover were rated for 104 broodsites. Some averages from these descriptions were: 57% cover by ground vegetation (includes logs and stumps), 25% duff, and 17% bare ground. Comparison with Table VIII shows that the first two are significantly different from the figures given for open habitats. Broods must have occurred more often in areas with heavy cover at ground level than chance would allow. The duff figure could be explained by assuming that younger broods avoided areas that were choked with dead plants and litter.

Some further analyses can be given to illustrate these preferences. The table below gives a rough breakdown on habitat at 244 broodsites. The categories are quite general because various methods were used to describe the habitat, depending on the observer.

Table IX. Approximate classification of habitat at 244 broodsites.

Open types of habitat - 80% of broods
- as in Very Open plot: 36%
- as in Open plot: 19%
- as in open plots but showing especially heavy cover at ground level: 16%
- within treeless open areas: 9%

Dense types of habitat - 6%
- as in Dense plot but with some openings: 2%
- heavy cover by conifers: 2%
- heavy deciduous thickets (alder, Rubus Parviflorus, Sambucus pubens, etc.): 2%

Other types of habitats
- dense patches of bracken: 8% *
- sedge (Carex spp.) areas: 2% *
- heavy cover by fallen logs: 4%

* these were within open habitats or in clearings in dense habitats

When these figures are compared with the fractions of the study area covered by each type of habitat, it is clear that open areas were favoured (90% of broods versus 65% of area, roughly). About 15% of these broods were immediately beside a moist area and, since this may not always have been mentioned, the percentage may have been higher than 15%. The ages of chicks in about 60% of the broods used in Table IX were estimated. Broods containing chicks less than a week old were found almost exclusively in areas of sparse vegetation (17 in open habitats, one in a bracken patch, one in an open area covered by log tangles, and one in heavy deciduous vegetation). This choice was obvious for broods of one to three weeks, as well (20 in open habitats or areas of bare ground, four in bracken patches, one in a log tangle). Broods having chicks over three weeks used more types of habitat but still favoured the open. This category showed very strong use of sites within open habitats that were well-vegetated at the ground level. Only 2% of all broods were found in vegetation that could be called Very Dense and about 3% were found on sites that would be called Dense habitat. The use of open habitat seemed to be more definite in broods than it was in lone females. Moreover, the selection seemed to be strongest in broods having younger chicks.

An attempt was made to compare the occurrence of plant species at broodsites with their occurrence on open habitats. After the percentages were corrected to allow for the difference in size of area sampled, it appeared that some species did occur more often at broodsites. Most prominent were Mahonia, Anaphalis, Hieracium, Vaccinium and Achlys species. The berries of Mahonia and the buds and leaves of Hieracium were probably important foods for older chicks, as the leaves of Anaphalis may have been. Vaccinium might have been used as a food plant but this could be an instance where the size of the individual plant compared to the quadrat size of one square yard gave a falsely low figure for the open plots. Similarly, the figures for Achlys on the plots were likely low due to the early appearance and withering of this annual, especially on the open plots. Some other species showed up more frequently in the broodsite analyses - Lysichitum americanum, Equisetum arvense, and Polystichum munitum, for example. There is a source of error in these cases since some quadrats on the plots were omitted as being atypical when they were located in a marsh or bog area. However, since broods often occurred in areas with widespread ground vegetation, these marshy species would be expected to show up more often at broodsites. From this, there is some indication that the dispersion of broods may have been partly determined by the presence of food plants.

For about 90 broodsites, the distance to the nearest moist area was measured in the field. As with lone females, the average here was about 95 ft., compared to 130 ft. for a set of random points. From preceding paragraphs it appears that older broods, at least, favoured areas with especially heavy vegetation on the ground. Moist areas <u>per se</u> were probably not important to females and juveniles, but such areas would show lush vegetation, and apparently this was what attracted the broods. There was no shortage of such spots on the Middle Quinsam range but on some breeding areas this might become the most important factor determining the dispersion of females and chicks. With the completion of this section it is clear that all grouse favoured habitats with sparse vegetation while on the breeding range. Beyond this, the location of broods appeared to be governed by the density of vegetation at the ground level, the amount of litter on the ground, and possibly by the presence of certain plants.

DISCUSSION

In this discussion I first review the material given in the Results to see [illegible]t agrees with or differs from the work of other investigators. Subjects are discussed in the order in which they were presented in the Results and some comments and speculations are presented in the review. I digress slightly to discuss the effect of dispersion on the regulation of breeding numbers, using mainly the experimental results. An attempt is then made to integrate all this information into an overall picture of dispersion on the breeding range. Finally, some comments are given on the adaptive significance of these processes.

The hooting of males has been used as a criterion of territorial behaviour in most studies on coastal blue grouse. This point should be discussed since there was little evidence in this study to show that hooting alone kept males apart. Hooting was performed almost exclusively by males that were localized on a given area and it appeared that any other males found on these areas were silent and presumably non-competitive because of immaturity. The mechanisms causing the observed spacing in resident males must have been threat displays, actual fighting, or avoidance of other males seen or heard. Hooting could have served to space males only if the last possibility was the most important one, since agonistic patterns of behaviour and hooting were quite distinct from each other. However, the correlation between hooting and the fidelity to an exclusive area was almost perfect. This suggests that, although hooting may not have been used to establish a territory, it was performed only by males that were on territory.

The trend toward uniform spacing shown by territorial males resembles that shown by Bendell (1954, 1955). This is apparently the first time that nearest-neighbour analyses, developed first by botanists (Dice, 1952; Hopkins, 1954), have been applied to an animal of this kind and there are some obvious weaknesses. The method does not allow for the instantaneous positions of birds but, since males focused their activities around a few central points rather than at the edges of their territories, application seemed worthwhile. The absence of any "boundary patrolling" suggests that the uniformity was a result of recognition and avoidance of neighbours, in the manner suggested by Lack (1954).

Territories were larger and more variable in size than those measured by Bendell (1954), indicating that size of territory was inversely proportional to density of territorial males. For example, better-known territories on the Middle Quinsam range were 3.7 acres on the average for a density of 0.15 territorial males per acre. On Bendell's (1954) study area the average for better-known territories was 1.3 acres, the density being about 0.4 per acre. It is interesting that males in the dense population showed an even closer return to territory in succeeding years than that found here. The indications are that older males were never driven from their territories by younger ones, and that avoidance caused a more rigid pattern of spacing to develop in the dense population. Either interaction was never strong enough to affect established territories or older males had an advantage in prior knowledge of an area or earlier arrival on an area.

This study seemed unique in showing at least a small fraction of yearling territory-holders. Again, this is probably dependent on density since Bendell found only one hooting yearling in three years of study. Boag (1964) recorded no yearlings holding territory in his population and felt that yearling males were forced into marginal habitats by the intolerance of adults. Although adults prevented some yearlings from establishing territory on the Middle Quinsam area, there was no evidence of eviction or increased mortality in these yearlings. Some yearlings probably did not descend to the breeding range but it is unlikely that the fraction here was as high as that suggested by Bendell (1954) or Buss and Schottelius (1954).

Experimental work confirmed that all the adults present were holding territories and contributing to the uniform spacing. The only alternative which cannot be dismissed is the possible expulsion of some males in April before extensive fieldwork was under way. This seems an unlikely possibility since wandering adults were never found outside of the period of migration, and since a high number of banded yearlings were recovered on territory in the year following their banding. Also, a good deal of space in open habitats was never used by males, and males were known to use a smaller area in seasons when they had closer neighbours. A short-term removal experiment on a more dense population (Bendell, 1954) gave results similar to this study except that there was no replacement of territorial males by yearlings. Bendell's population apparently had the highest density ever recorded for blue grouse so it seems doubtful that surplus groups of adult males are a feature of blue grouse populations on their breeding ranges. As might be expected, interaction in the more dense population first affected the behaviour of yearling males. Whether the interaction associated with even higher numbers would lead to more use of emptied areas in succeeding years is still an open question.

The selection of open elevated areas for territories and the choice of spots within the territory for hooting and displaying are similar to the findings of other workers. However, the clear choice of habitat by yearling males has not been noticed or discussed before. The use of elevated areas for hooting has been mentioned by Caswell (1954) and Schottelius (1951) while Edson (1925) and Steinhoff (1958) have commented on the correlation between height of land and local occurrence of blue grouse. Boag (1965) showed that territory selection in his population could be correlated with density of vegetation (favoured spots having about 50% canopy cover) but not with plant species. Bendell (1954) studied the vegetative structure of territories and pointed out that territorial boundaries were not limited by types of vegetation. The present work agrees fairly well with both these studies except that the presence of Very Dense vegetation did seem to determine the boundaries of some territories. Use of open areas within dense habitat was also noticed by Heebner (1956). Descriptions of hooting sites within territories correspond well with those mentioned by Bendell (1954) and Blackford (1958, 1963). These preferences seem to be shown by males in a number of populations, both of coastal and interior races.

Apparently the extreme openness of the habitat caused some groups of males to develop a type of behaviour showing some points in common with the communal behaviour of the "prairie" grouse (Lyrurus tetrix, Tympanuchus cupido, Pedioecetes phasianellus, and especially Centrocercus urophasianus), discussed by Ammann (1957), Hamerstrom and Hamerstrom (1960), Hart et al (1950), Hohn (1953), Scott (1950), and Wynne-Edwards (1962). This bears out the suggestion that the type of breeding display in tetraonids can be influenced by the type of habitat used as breeding range (Hoffman, 1956). In dispersion and habitat, Dendragapus, Tetrao (Koskimies, 1957), and Canachites (Lumsden, 1961) species are probably intermediate between solitary forms such as Bonasa umbellus (Darrow, 1950; Bump, 1950; Palmer, 1961) and the "lek" or communal forms mentioned above. The fact that interior races of blue grouse, using grassland or other very open areas for breeding, show a tendency to use communal display areas bears out the present observations and supports the thesis of Hoffmann. Coastal blue grouse are obviously closer to the solitary forms and show no use of any traditional display grounds. The "groups" here probably represent clusters of territories around a favourable area, as suggested by Koskimies (1957) and Svardson (1949).

The fidelity of juveniles to their natal area has been the subject of argument in the literature. It appears now that most authors would support the suggestion made here, that juveniles disperse widely between their first and second summers (Bauer, 1962; Bendell, 1954; Boag, 1965; Mussehl, 1960). It must be pointed out that the assumed dispersal tendency could have resulted from incorrect assumptions about the mortality of juveniles. The few data available suggest that chicks do not return to the same habitat as found at their area of birth. The unique data from this study on movements of yearling males show that the locations of males became more localized with increased age up to adulthood, depending largely on when the males took up territory.

Lack of aggression between hens seems to be a property of all breeding populations of blue grouse. Bendell (1954) mentions one case of apparent hostility between hens and I have found no others in the literature on free-ranging populations. If hens met often at feeding and dusting areas, or near hooting males, one might expect some sort of dominance pattern to arise. This may have happened but, because no fighting was observed and hens were seen together on occasion, it seems more probable that hens merely ignored or avoided each other when they met. Other authors have noticed intermingling of broods, as well as lone hens travelling with broods, and have presumed that adoption of orphaned chicks would occur (Bendell, 1954; Fowle, 1960; Mussehl, 19' ; Wing et al, 1944).

Very little has been published on the habitat preferences of females prior to nesting or during incubation. Nest-sites have been studied in a little more detail and the only feature common to all reports is an apparent preference for open habitat with logs, stumps, or low vegetation as cover for the actual site (Bendell, 1954; Caswell, 1954; Mussehl, 1960). Various workers have related the location of broods to such factors as presence of certain plants (for example, Amelanchier or Ribes spp.), nearness of free water, or to the degree of coverage by vegetation (Bauer, 1962; Bendell, 1955; Marshall, 1946; Mussehl, 1960 and 1963; Wing et al, 1944). Certain plants may have helped determine the dispersion of broods here but they were not the expected fruit or berry-carrying species. Coverage by vegetation was apparently very important, and this agrees with other studies. If the "free-water" areas of other authors showed heavy surrounding vegetation at ground level then this preference would be comparable to results given here.

It is useful to question whether any of the factors affecting dispersion might also have limited breeding numbers. Territorial behaviour seemed the only factor capable of doing this. I have suggested that the failure of many yearlings to hold territories was as much due to their immaturity as to the influence of resident males. Territoriality would limit productivity only if both sexes were monogamous and hens were pairing exclusively with territorial males. This was not the case and there was no evidence of any lowering of nesting or rearing success by the activities of males. Since males took no part in the defence of females, nests, or chicks, territoriality apparently served only to isolate males sufficiently to prevent any interference with displaying and mating. This function has been suggested for other species by a number of authors, for example - Lack (1939), Nice (1941), Pitelka (1959), Tinbergen (1956). It is very unlikely that interaction on this breeding range was having any regulatory effect on density as suggested for other species by Choate (1963), Jenkins (1961), Jenkins et al (1963), Kluyver and Tinbergen (1953), and Tompa (1962, 1964).

On this breeding range, what overall pattern of dispersion is revealed when both sexes and all age-groups are considered together? This is best described by considering the pattern found in favourable habitat, and then that found in unfavourable habitat. The dispersion over favoured areas apparently took the form of small groups of birds spaced in a near-uniform distribution, each group consisting of a territorial male plus any yearling males and lone females that were attracted to him. The two latter types probably shifted from group to group, although the females' positions would soon become fixed by their nesting. Midway in the season another pattern involving aggregations of birds was superimposed on the first, the groups here being broods (with their females) moving randomly with respect to each other and the males. Later in the season the near-uniform pattern began to break up as males migrated. The pattern visualized is an idealistic one since groups would constantly be breaking and reforming as birds moved to their individual feeding or roosting areas.

On less favourable areas the dispersion probably took the form of randomly-located males, the spacing having changed due to attrition and movement of remaining males to any nearby remnants of favourable habitat. As the area became less favourable the yearling male, and then the female and juvenile components would disappear through the action of habitat selection and possibly mortality.

These patterns of utilization seem adaptive when the nature of the habitat is considered. Coastal forests which have been logged or burned by forest fires must be near-optimal breeding range judging by the population expansions and high densities that occur there. The dispersal of juveniles, the habitat preferences of yearling males, and the tendency for lone females to occur on territories would allow blue grouse to make rapid use of open areas made available to them. The stability brought about in some species by pair-bonding and expulsion of certain members would seem ill-adapted to a situation calling for quick settlement and expansion of numbers. One might expect to find no pair-bonds, no surplus birds, and no unmated females in such a situation.

Most of the favourable habitat available to these birds would eventually become unfavourable through regeneration and succession. Aldrich (1963) and Brooks (1926) mention the use of natural openings in mature coastal forest by the _fuliginosus_ race. At times these openings and ridges, perhaps together with alpine areas, would be the only breeding habitat available. The preference for open and elevated areas shown by territorial males would be of particular value at such times. Large open areas are constantly appearing in coastal forests through the action of fires, slides, and human activities. The blue grouse of the forests seem to maintain themselves by quickly exploiting such areas.

SUMMARY AND CONCLUSIONS

An attempt has been made to analyze the dispersion of a population of blue grouse (Dendragapus obscurus fuliginosus) on its breeding range on east-central Vancouver Island. To do this, grouse were observed and banded over an area of about five square miles, the greatest effort being concentrated on a number of plots set in different habitats. The effect of intraspecific interaction on dispersion was studied by examining the density, behaviour, locations, and movements of males, females, and juveniles. The effect of habitat selection was studied by comparing numbers and locations of birds in open and dense habitats. The influence of both these factors on the dispersion of males was investigated by removing males from plots in open and dense habitats starting at the beginning of each breeding season.

Interaction had some pronounced effects on the dispersion of males. All the adult males and a few of the yearling males were territorial, and this group approached uniformity in their distribution. Within a given season, males removed from their territories were seldom replaced by other adults suggesting that no surplus of non-territorial adults was present. However, the experiment showed that about half of the yearling males were prevented from establishing territory by the presence of territorial males, and that these yearlings were attracted to the vicinity of territorial males. Removal also showed that the location of territories by newly-adult males did not depend noticeably on the number of territorial males already present on a given area, even though the tendency toward uniform spacing was preserved. Comparison with other studies indicated that the sizes of territories and possibly the fraction of yearling males in the population were inversely proportional to the density of territorial males.

Females restricted their activities to a given area while on the breeding range but they were not territorial. Prior to nesting, females apparently stayed near territorial males but there was no sign of any lasting pair-bonds. After the time of hatch the positions of females and broods bore no relation to each other or to the positions of males.

All birds, yearling males particularly, showed a preference for open types of habitat rather than dense. This choice was confirmed by a decline in numbers on the study plots in the most dense type of habitat. When compared with randomly chosen points, territories were found more often in areas with sparse vegetation, elevated points, and patches of open ground. Within open habitats, nests were usually located where cover by logs, stumps, and ground-level vegetation was higher, and cover by dead plants and litter was lower than normally found in these same habitats. Broods, although found most commonly in sparse habitats, were associated with moist areas and other areas having heavy cover by vegetation at the ground level.

There was some evidence to suggest that juveniles dispersed widely between their first and second summers. In their third (first adult) summer males usually returned within one-half mile of the positions they used as yearlings. Once territories were established, the adult (or yearling) owners returned very closely to them in succeeding summers. Females past the age of one year showed some fidelity to their earlier locations, the closeness of return being about that of new adult males.

The dispersion of the population can be described, rather artificially, by considering the birds to be in two types of aggregations, A and B. Type A groups were distributed somewhat uniformly, consisted of territorial males plus other birds that were attracted to them, and were the major groupings during the first half of the breeding season. Type B aggregations were broods, moving randomly with respect to other birds, but holding to a home range from the time of hatch to migration. The habitat preferences mentioned would cause the density of these groups to vary over the breeding area. As areas grew unfavourable, members of the groups would drop out until only the older males remained.

Results on movements and choice of habitat suggest how blue grouse might move into newly-opened areas in the coastal forests. Many features related to the dispersion of the population seem to be adaptations allowing grouse to use rapidly-changing habitats. Among these are the dispersal of juveniles, the choice of sparse vegetation by yearling males, the tendency for hens to stay near territories prior to nesting, and the lack of any interaction within the summer population that might cut down productivity.

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APPENDICES

Appendix 1. Percent coverage shown by various elements along line-intercepts, 1962. Key given below:

	Line No.	F	C	H	P	W	A	V	S	B	L
Open plot	1	28.4		1.8		4.9			7.6	24.0	6.3
	2	21.2				9.2			15.4	47.7	10.7
	3	23.0				10.5			27.6	21.4	16.0
	4	8.0			1.7	20.7			13.8	48.9	8.4
	5	31.6				17.2			16.7	41.0	13.7
	6	37.9				13.5			17.9	30.7	9.7
	8	30.1				8.2		1.9	0.9	20.2	15.3
	9	18.9				11.1	14.5		21.2	35.9	4.4
	12	12.9	2.5		0.7	28.4	1.0		17.8	4.9	14.2
	13	38.3		1.8		10.7			18.1	45.3	0.7
	15	42.4	6.3			27.0		0.6	2.8	3.8	9.1
	x-1	18.4	8.6	0.8		18.6			24.9	16.2	24.1
	x-2	30.4				9.6			7.9	27.4	11.9
Very open plot	1		0.3			6.0			28.1	36.4	14.1
	2	0.8				9.8			21.2	7.2	24.8
	3					18.5			14.9		11.1
	4					16.6			2.9		18.7
	5	4.9				2.7		0.5	13.8	18.1	12.7
	6					26.0				38.4	7.8
	7	2.8				10.2			9.6	18.8	2.8
	8	0.7	0.5	2.1		16.1			0.8	0.9	18.6
	9	0.8				17.5			0.8	20.9	14.8
	12	1.3				13.2		0.7	31.7	10.2	29.4
	13	4.0		1.1		7.2			10.1	23.2	8.6
	14					9.0				16.8	16.3
	15	0.8				15.0			2.2	20.3	4.7
Very dense plot	1	92.4	-	-		16.6		4.2	37.2		11.3
	2	58.3	-	-		25.2		3.0	35.2		17.3
	3	79.3	-	-		7.4			38.4		14.2
	4	72.4	-	-		29.7		7.1	21.9	1.3	11.4
	5	69.6	-	-		9.1	24.7		6.7	14.7	13.2
	6	75.4	-	-		26.1		4.5	4.2	4.3	22.5
	7	80.9	-	-	-	x	34.5	x	18.2	7.2	30.6
	8	69.2	-	-	-	x	37.4	x	27.1		12.6
	9	94.1	-	-		5.9		2.1	51.3	14.7	4.6
	11	51.6	-	-		18.0		1.9	68.2	3.3	8.3
	12	84.6	-	-		8.0			34.6	9.6	8.0
Dense	1	3.4	39.8	23.1	12.4	12.0		3.7	44.4	1.2	19.4
	2	83.4	-	-	-	12.8		6.3	41.7	29.4	14.3
	5	8.3	10.5	8.4	1.4	22.7		4.3	27.7	1.7	45.9
	6	3.0	2.6	5.6		41.9		2.4	15.3		19.3
	7	40.8	-	-	-	13.5		1.6	32.0	3.8	17.0
	9	14.5	24.0	9.3		21.4		1.1	25.5	22.5	13.5
	10	2.4	40.3	5.4		6.6		4.3	31.5	10.7	24.6

	Line No.	F	C	H	P	W	A	V	S	B	L
	11	22.6	-	-	-	25.6	1.8	0.4	19.0	78.8	14.1
	12		15.2	19.6	2.5	15.0			14.8	26.3	30.7
	13	53.1	-	-	-	31.1		0.7	2.6	11.5	15.9
	14	51.8	-	-		36.4		1.1		5.8	30.1
	15	6.7	23.1	5.2		42.1	2.1	4.0		5.4	40.7
(Open)	11	1.6	40.5	1.0		21.9		3.4	25.0		33.2

Key:

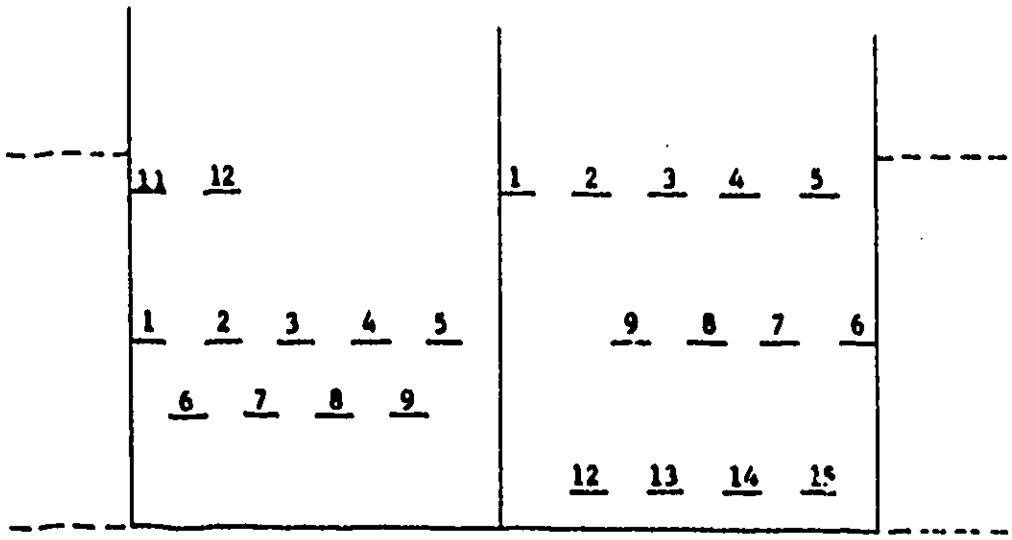
F - Douglas fir
C - cedar
H - hemlock
P - pine
W - willow
A - alder
V - Vaccinium
S - salal
B - bracken
L - logs and stumps

\- included under Douglas fir in this case
x included under alder in this case

Note:

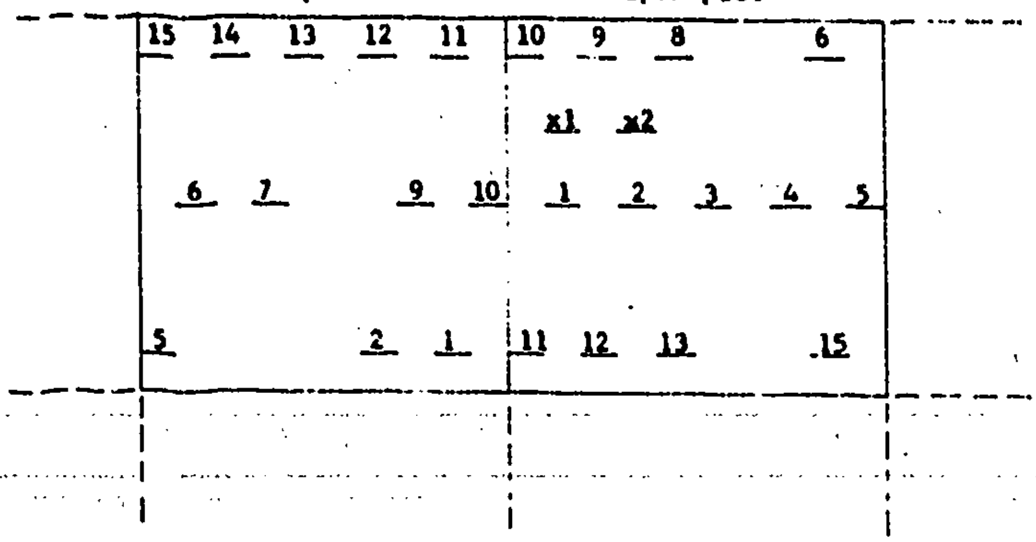
Any line or quadrat that fell within an area showing atypical vegetation (peat bog, alder grove, etc.) was omitted from these tables.

Appendix 1, cont. Positions of hundred-foot lines used for analysis of vegetation on study plots, 1962.



Very dense plot   Very open plot

Dense plot   Open plot



Appendix 2. The occurrence of certain plant groups and species on quadrats located within the study plots.

	Open plot	Very open plot	Very dense plot	Dense plot
Total number of quadrats	63	71	60	68
Percentage occurrence of:				
All coniferous species	71%	32%	97%	78%
All deciduous species	71	72	78	85
Douglas fir	67	28	22	12
Red cedar	3	7	53	60
Western hemlock	0	1	88	32
Pinus species	0	0	0	4
Salix species	67	68	57	76.5
Red alder	0	0	8	0
Vaccinium species	8	13	35	46
Bracken	73	58	17	32
Salal	57	46.5	65	59
Mahonia species	17	28	18	32
Anaphalis margaritacea	44	56	50	46
Rubus vitifolius	70	89	85	81
Hypochaeris radicata	63*	63	53	32
Hieracium species	29*	32	30	32
Achlys triphylla	0*	0*	-	21

* based on 41 quadrats rather than total given

Appendix 3. Total number of hours spent by all observers on study plots, 1959-1962.

(Figures represent totals up to the end of June for each year and are rounded off to the nearest hour.)

	1959	1960	1961	1962	Total
Hours spent on:					
Open control plot	9	15	18	60	102
Very open removal plot	5	14	3	68	90
Very dense removal plot	2	14	3	12	31
Dense control plot	15	17	3	18	53
Plots (main controls)	18	23	29	11	
Plots (removal)	17	19	44	14	
Plots - not known specifically	17	18	14	11	
Total control	42	55	50	89	236
Total experimental	24	47	50	94	215
Total for all plots	83	120	114	194	

Appendix 4. Dates on which removal plots were visited, up to end of June, 1959-1962.

Month	Date	1959	1960	1961	1962
March	15		x		
	16		x		
	17		x		
	18		x		
	19				
	20				
	21		x		
	22				
	23				
	24		x		x
	25		x		x
	26				x
	27		x		x
	28				
	29		x		
	30				
	31				
April	1				
	2				
	3				
	4				
	5		x		
	6				
	7		x		
	8				
	9				
	10		x		
	11				
	12		x		
	13				
	14		x		
	15		x		x
	16		x		x
	17		x		x
	18		x		x
	19				
	20				
	21		x		
	22				
	23				
	24				
	25		x		
	26		x		
	27		x		
	28				
	29				
	30				
May	1				x
	2		x	x	x
	3			x	x
	4			x	x
	5			x	x
May	6		x	x	x
	7		x		x
	8			x	
	9			x	x
	10		x	x	x
	11		x		x
	12		x		x
	13		x		x
	14				x
	15				x
	16	x	x		x
	17		x		x
	18		x		x
	19	x		x	x
	20	x			x
	21				x
	22	x		x	x
	23	x			x
	24				x
	25		x	x	x
	26	x		x	
	27	x	x		x
	28		x	x	x
	29			x	x
	30		x	x	x
	31		x	x	x
June	1	x			x
	2	x	x		x
	3				
	4				
	5	x			
	6			x	x
	7			x	x
	8	x			
	9			x	x
	10	x		x	
	11			x	x
	12				x
	13			x	
	14				x
	15		x		x
	16	x	x		x
	17	x			
	18		x		x
	19				
	20			x	x
	21			x	x
	22		x	x	
	23	x		x	x
	24				x
	25				x
	26	x			x
	27			x	x
	28			x	

Appendix 5. Comparison of vegetation and topography at known territories and randomly-chosen points, 1962. (Number of samples is given in brackets for each category.)

Feature studied	Territories		Random points		Diff.*
Type of vegetation	(75)		(68)		
- very open		57%		28%	Sig.
- open		20		29	
- dense		16		21	
- very dense		1		7	
- mixture of two of four above		5		9	
- other type (alder, swamp, etc.)		1		6	
Cover by trees and shrubs	(75)	41%	(68)	51%	Not sig.
Cover by ground vegetation	(75)	25	(65)	38	Sig.
Dispersion of trees and shrubs	(74)		(60)		
- spaced fairly evenly		45		37	
- slightly clumped		20		33	
- in clumps or patches		27		30	
- thickets or patches caused by road or grade		8		0	
Topography	(75)		(68)		
- top of plateau, knoll, or hill		25%		3%	Sig.
- steep slope, hillside		52		53	
- slight slope		12		24	
- flat		8		13	
- in slight hollow or depression		3		3	
- in marked hollow or depression		0		4	
Mean height of trees	(75)	10.2 ft.	(68)	11.8 ft.	

* Differences tested for significance at 5% level by chi-square test.

Appendix 6. Approximate analyses of some vegetative and topographic components at positions of hooting and silent males (based on 172 observations of hooting males and 130 observations of silent males).

	Hooting	Silent
Mainly coniferous cover	21%	31%
Dense cover of willow (often in thickets)	9	14
Sparse cover of willow (as in very open zones)	15	23
In definite treeless clearing	11	4
Alder thicket	2	5
Dense bracken cover (later in year)	5	8
Dense fallen log tangles	4	4
Swamp edge, creek or slough area	0	12
Grade or road edge	10	12
Knoll, elevation, mound	12	none noted
Under conifer	19	19
On log or stump	15	3
Beside (under) log, stump, root	12	15

Appendix 7. Estimation of new males on nine control plots in Very Open, Open, and Dense habitat. See section comparing control and experimental areas.

Assume 25% mortality rate in males.

Situation in: 1959 - 24 males present
- 5 males accidentally killed
- apply 25% rate to 19 males
- assume 14 return in 1960

1960 - 32 males present
- 32 less 14 gives 18 new males
- 4 males accidentally killed
- assume 21 return in 1961

1961 - 31 males present
- 31 less 21 gives 10 new males
- assume 23 return in 1962

1962 - 33 males present
- 33 less 23 gives 10 new males

Total number of new males by this method:

38 for three breeding seasons over nine study plots

Appendix 8. Calculation of death rate for banded adult males. A few silent males that were banded late in the breeding season have been omitted from the calculation.

Adults banded in 1959	25	age 2 years "plus"
Returned in 1960	22	
Left alive in 1960 (i.e., not collected)	21	age 3 years "plus"
Males from this group returned in 1961 (none collected)	18	age 4 years "plus"
Males from this group returned in 1962	14	

Adults banded in 1960	31	age 2 years "plus"
Returned in 1961	24	
Left alive in 1961	21	age 3 years "plus"
Returned in 1962	13	

Adults banded in 1961	28	age 2 years "plus"
Returned in 1962	17	

Total banded in 'two year plus' group - 84 males
Total returned out of this group - 63
Death rate for the intervening year - 25%

Total banded in 'three year plus' group - 42
Total returned out of this group - 31
Death rate - 26%

Total banded in 'four year plus' group - 18
Total returned out of this group - 14
Death rate - 22%

Overall yearly death rate approximately .. 25%.